

PHYLOGENY OF THE PLESIOPIDAE (PISCES: PERCIFORMES) WITH EVIDENCE FOR THE INCLUSION OF THE ACANTHOCLINIDAE

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ABSTRACT

Cladistic methods are used to investigate phylogenetic relationships of the Indo-Pacific marine fish family Plesiopidae. Using multiple outgroups, osteological and myological characters indicate that plesiopids are monophyletic only with the inclusion of the Acanthoclinidae as the sister group to the genus *Plesiops*. A new classification lowers the Acanthoclinidae to subfamilial rank, and other monophyletic units are recognized at this same rank to produce the following phylogenetically sequenced classification (included genera in parentheses): Trachinopinae (*Trachinops*), Assessorinae (*Assessor*), Paraplesiopinae (*Paraplesiops*, *Callopleysiops*, *Steeneichthys*), Fraudellinae (*Fraudella*), Plesiopinae (*Plesiops*), Acanthoclininae (*Acanthoclinus*, *Belonepterygion*, *Belioops*, *Acanthoplesiops*). This phylogeny suggests that egg mass guarding is plesiomorphic for the family, and that oral incubation in *Assessor* is autapomorphic. A diagnosis for the newly defined family is provided.

The family Plesiopidae, commonly called longfins, prettyfins, devilfishes, or roundheads, comprises a morphologically diverse group of percoid fishes found in the Indo-Pacific region. There are about 30 species in the family as currently recognized. Adult size ranges from 30 to 300 mm in standard length, and body form varies from narrow and elongate to bulky and heavy bodied. The species also vary considerably in behavior, from diurnal schooling to nocturnal solitary habits. Most are found in relatively shallow water (to 30 m) on coral or rocky reefs. The group is unusual among marine percoids in having demersal eggs with adhesive filaments, characteristic of only four other percoid families: Acanthoclinidae, Grammatidae, Opistognathidae, Pseudochromidae.

First introduced as a suprageneric taxon by Günther (1861), the Plesiopidae are usually considered to be a basal percoid group and placed near the family Serranidae in most taxonomic summaries (Nelson, 1984). However, the suborder Percoidei itself has proven difficult to define, and is probably not monophyletic. As noted by Johnson (1984), the questionable integrity of the Percoidei has made it a convenient repository for so-called generalized perciform families that cannot obviously be placed elsewhere. Such has been the fate of the Plesiopidae. Little attention has been given to the phylogenetic position of plesiopids with respect to other percoid families. Springer et al. (1977) explored possible relationships among the basal percoid families Pseudochromidae, Acanthoclinidae, Grammatidae, and Plesiopidae, plus the Opistognathidae, but did not reach any firm conclusions. Johnson (1984) briefly noted that these families are the only percoids that possess demersal egg masses, and suggested that this might be a derived feature uniting them. Mooi (1990) examined the egg surface morphology of these families, but uncertainty in determining homology and polarity of character states hampered phylogenetic analysis. Relationships among these taxa have not been rigorously tested by detailed osteological or myological study.

The composition of the Plesiopidae itself has been questioned, perhaps because of the diversity within the family. Hoese and Kuitert (1984) provided the most recent overview of the generic composition and included *Assessor* Whitley, 1935, *Callopleysiops* Fowler and Bean, 1930, *Fraudella* Whitley, 1935, *Paraplesiops* Bleeker, 1875, *Plesiops* Cuvier, 1816, and *Trachinops* Günther, 1861. However,

they noted (Hoese and Kuitert, 1984: 8) that: "Further studies are necessary to determine the relationships of *Assessor*, *Trachinops* and *Callopleiops* to the three [other] typical plesiopid genera." Springer (1982) had already indicated that he did not believe that the family was monophyletic, but both his and Hoese and Kuitert's (1984) reservations appear to be based on phenetic dissimilarities between the taxa rather than any cladistic evidence. Allen and Randall (1985) added a seventh genus to the family, *Steeneichthys*, believing it to be most closely related to *Plesiops*, but this too was a phenetic assessment rather than a cladistic one.

In this study, cladistic methods are used to tackle both the phylogenetic position of the Plesiopidae within the Percoidae and its generic composition. I first summarize previous views of plesiopid taxonomy and classification. Using multiple outgroups, including those percoids with demersal eggs, I present a phylogeny of the Plesiopidae using osteological and myological features. I hypothesize that the Plesiopidae as currently defined are paraphyletic, and become monophyletic only upon the inclusion of the Acanthoclinidae. This phylogeny is then used to construct a new classification for the Plesiopidae and to provide a diagnosis for the family based on derived features. It also is used to comment further on previous hypotheses on evolution of reproductive behavior in percoids.

METHODS AND MATERIALS

Osteological and Myological Preparations.—Osteology of plesiopids and other taxa was examined by two major techniques. The bulk of specimens were cleared and stained for bone and cartilage, following the methods of Dingerkus and Uhler (1977) or Taylor and Van Dyke (1985). These specimens were dissected to various degrees, but usually the suspensorium, suborbitals, hyoid apparatus, and gill arches were removed first, followed by the pectoral and pelvic girdles. Occasionally the cranium was removed from the axial skeleton, and for some species a spine-bearing dorsal-fin pterygiophore was removed. Some specimens were examined using soft x-ray radiography.

Pelvic musculature was examined after the pelvis was removed and stained with a variation on Lugol's solution (Bock and Shear, 1972). Muscle bundles were identified, drawn under a binocular dissecting microscope through a camera lucida, and then removed to reveal deeper muscle groups. Muscles were often examined before clearing and staining for osteological study. Muscle terminology follows that of Winterbottom (1974).

Phylogenetic Analysis.—External, osteological, and myological characters were analysed following the principles of phylogenetic systematics (cladistics) to generate hypotheses of relationships. The general methodology was first outlined in English in Hennig (1966), but has subsequently been modified by numerous authors. Wiley (1981) best summarizes the techniques and philosophy that I embrace. The outgroup method of Watrous and Wheeler (1981), rearticulated by Mooi (1989), was used to polarize characters and provide evidence of relationships based on derived (apomorphic) features. Features are discussed first as their primitive state under "Plesiomorphy," and then as the derived condition under "Apomorphy." Where homoplasies (incongruences) could not be redefined as non-homologous conditions on the basis of ontogenetic or other morphological criteria, they are discussed under the subheading "Homoplasies" and sometimes further explored under "Remarks" for a particular character. For some features, the global parsimony techniques of Maddison et al. (1984) were employed, although biological explanations of homoplasy (i.e., as structural non-homology) were preferred over parsimony explanations. Initial cladistic analyses via Hennigian argumentation were corroborated by analysis employing the branch-and-bound option of PAUP (Phylogenetic Analysis Using Parsimony) version 2.4.1 of D. L. Swofford (Illinois Natural History Survey, Champaign, Illinois). This option is guaranteed to generate the shortest tree(s). A consistency index and a retention index (Farris, 1989) are presented for all analyses.

A phylogenetic classification of the plesiopid taxa is presented in this study. Only monophyletic groups are recognised (i.e., all descendants of a given ancestor). The classification follows the conventions for an annotated Linnaean system as outlined by Wiley (1981).

Material Examined.—Material is listed alphabetically by family, then alphabetically by species. Each species is followed by a catalogue number, number of specimens, and size range in mm SL. Following the size is a notation in square brackets indicating whether the material was examined for osteological features (CS = cleared and stained, X = x-ray radiograph) and/or myological features (M). For the genus *Plesiops*, x-ray radiographs were available for all species, but material is too numerous to list;

a full account is available from the author and will appear in a forthcoming revision. Museum acronyms follow Leviton et al. (1985). APOGONIDAE: *Pseudamiops gracilicauda*, ROM 908CS, 28.0 [CS]; *Sphaeramia nemaptera*, ROM 780CS, 5: 40.0–68.0 [CS]; CALLANTHIIDAE: *Callanthias allporti*, ROM 1336CS, 57.1 [M, CS], WAM P.25200, 127.0 [CS]; *C. legas*, SAM 25022, 133.0 [CS]; *C. parini*, ANSP 152995, 153.0 [CS]; *C. platei*, SIO 65-629, 114.0 [CS]; *C. ruber*, ISH 220/77, 93.0 [CS]; *Grammatonotus laysanus*, BPBM 22757, 93.0 [CS]; *G. crosnieri*, MUSORSTOM 2, 95.0 [CS]; CLINIDAE: *Gibbonsia metzi*, ROM 859CS, 86.0 [CS]; GRAMMATIDAE: *Gramma loreto*, ROM 997CS, 4: 39.6–43.5 [CS], ROM Uncat., 62.5 [M], ROM 31324, 44.8 [M]; *G. melacara*, ANSP 117359, 55.7 [M], ROM 1006CS, 50.0 [M, CS]; *Lipogramma anabantoides*, USNM 216405, 17.0 [CS]; *L. klayi*, ANSP 127671, 2: 23.8 [M, CS]–27.3 [M]; MORONIDAE: *Morone americana*, ROM 349CS, 4: 40.0–52.3 [CS], ROM 29525, 120.1 [M], ROM 43403, 115.8 [M], ROM 1064CS, 2: 70.0–89.0 [CS]; *M. chrysops*, ROM 27793, 118.9 [M]; NOTOGRAPTIDAE: *Notograptus guttatus*, ROM 717CS, 82.2 [CS]; OPISTOGNATHIDAE: *Opistognathus darwiniensis*, ROM 1329CS, 51.0 [M, CS]; *O. maxillosus*, ROM 1330CS, 58.0 [M, CS], ROM 40692, 67.1 [M]; *Opistognathus* sp., ROM 778CS, 54.0 [CS]; PLESIOPIDAE: *Acanthoclinus fuscus*, NMNZ P.14719CS, 3: 19.0–60.0 [M, CS], NMNZ P.14719, 74.2 [M], USNM 200547, 2: 68.7–84.2 [M]; *A. littoreus*, ROM 1335CS, 2: 58.0–72.0 [M, CS]; *Assessor macneilli*, ROM 890CS, 31.5 [CS], USNM 269466, 3: 43.0–48.9 [M, CS]; *Belonepterygion fasciolatum*, ROM 1212CS, 30.7 [M, CS], ROM 1328CS, 39.7 [M, CS]; *Callopleysiops altivelis*, AMS I.15684-032, 77.4 [M], ROM 894CS, 50.0 [CS], ROM 1334CS, 69.5 [M, CS], USNM 217964, 65.2 [M]; *Fraudella carassiois*, QM IA.4788, 5: 16.0–25.0 [X], QM IA.6302, 7: 28.5–45.0 [X], QM I.10783, 36.5 [X], QM I.19760, 45.0 [M, CS], QM I.19760, 6: 26.9–45.0 [X], QM I.21376, 2: 32.3–46.0 [X]; *Paraplesiops alisonae*, NMV A2259CS, 64.5 [M, CS], NMV A2259, 63.8 [M], WAM P.27578-001CS, 59.5 [M, CS]; *P. bleekeri*, AMS I.20815-001CS, 29.0 [M, CS]; *P. meleagris*, WAM 26812-007CS, 70.0 [M, CS]; *P. poweri*, AMS I.17445-006, 66.3 [M], USNM 274578CS, 2: 47.8–50.5 [M, CS], USNM 274579, 95.0 [M]; *Plesiops cephalotaenia*, ROM 1325CS, 53.0 [M, CS]; *P. coereruleolineatus*, ANSP 108721CS, 2: 9.3–11.0 [CS], ANSP 108721, 53.7 [M], ROM 776CS, 4: 21.3–46.0 [CS], ROM 1324CS, 10.0 [CS], ROM 1326CS, 10.8 [CS], ROM 1337CS, 4: 12.6–20.0 [CS], USNM 264168CS, 4: 15.0–53.0 [CS], USNM 288548CS, 10.0 [CS]; *P. corallicola*, AMS I.15360-042CS, 70.0 [CS], AMS I.15360-042, 4: 74.5–94.3 [M], ANSP 51528, 36.2 [M], ANSP 108275, 55.5 [M], ANSP 122597CS, 55.0 [CS], ANSP 122597, 89.4 [M], LACM 6674-44, 107.0 [M], ROM 893CS 34.5 [CS], USNM 154392, 110.5 [M], USNM 274574, 2: 27.5–65.0 [CS]; *P. genaricus*, AMS I.19483-026CS, 2: 50.0–59.0 [M, CS]; *P. gracilis*, CAS 67423CS, 2: 41.8–63.5 [M, CS]; *P. insularis*, AMS I.17363-004CS, 40.0 [M, CS], AMS I.17363-004, 2: 60.0–94.0 [M]; *P. multisquamata*, RUSI 76-16CS, 49.5 [M, CS], USNM 246690, 123.6 [M]; *P. nakaharae*, IORD 80-167, 107.4 [M, X]; *P. nigricans*, USNM 274569CS, 63.2 [M, CS], USNM 274569, 68.8 [M]; *P. oxycephalus*, USNM 274575CS, 63.0 [M, CS]; *Plesiops* sp. 1, ROM 60180, 62.0 [M]; *P.* sp. 2, USNM 146471, 46.3 [M]; *P.* sp. 3, COM 71-PE3, 98.2 [M], USNM 320020, 110.3 [M]; *P.* sp. 4, USNM 313012, 47.5 [M]; *P.* sp. 5, USNM 315537, 37.8 [M]; *P.* sp. 6, AMS I.15681-043, 2: 47.3–57.7 [M], CAS 67574 60.0 [M], ROM 903CS, 3: 21.0–82.0 [CS]; *Steeneichthys plesiopsus*, BPBM 20012CS, 30.2 [M, CS], BPBM 20012, 2: 24.1–29.2 [X], BPBM 24110, 2: 21.3–25.6 [X], ROM 1331CS, 25.8 [M, CS], USNM 242118, 25.4 [X], USNM 288926, 3: 10.5–18.4 [X]; USNM 288927, 20.1 [X], WAM P.28031-018, 26.3 [X]; *Trachinops brauni*, AMS I.20845-018, 47.3 [M], ROM 1327CS, 2: 40.0–46.0 [M, CS]; *T. caudimaculatus*, ROM 49183, 2: 50.7–60.5 [M]; *T. noarlungae*, ROM 1332CS, 2: 41.0–48.0 [M, CS], ROM 49180, 51.0 [M]; POMACENTRIDAE: *Eupomacentrus albifasciatus*, ROM 37300, 87.0 [M]; PSEUDOCROMIDAE: *Anisochromis straussi*, ROM 557CS, 24.2 [CS]; *Chlidichthys inornatus*, ROM 857CS, 3: 30.0–37.0 [CS], ROM 46327, 36.8 [M]; *Congrogadus spinifer*, ROM 855CS, 2: 58.0–67.0 [CS]; *Cypho purpurascens*, ROM 1338CS, 2: 37.4–50.0 [M, CS], ROM 46753, 53.5 [M]; *Labricinus lineatus*, ROM 684CS, 95.0 [CS]; *Ogilbyina queenslandiae*, ROM 685CS, 84.0 [CS]; pseudochromine new genus *A. porphyreus*, ROM 1333CS, 38.0 [CS], ROM 55450, 44.4 [M, CS]; *Pseudochromis aldabraensis*, ROM 177CS, 62.0 [CS], ROM 40009, 70.0 [M]; *P. cyanotaenia*, ROM 46831, 39.5 [M]; *Pseudochromis marshallensis*, ROM 1339CS, 5: 14.1–35.0 [CS], ROM 53982, 46.9 [M]; *Pseudoplesiops rosae*, ROM 46723, 8: 15.7–20.6 [M]; *P. typus*, ROM 858CS, 49.0 [CS]; SERRANIDAE: *Pseudanthias squamipinnis*, ROM 1344CS, 2: 33.2–45.0 [CS]; *Belonoperca chabanau-di*, ROM 46765CS, 33.8 [CS]; *Cephalopholis leopardus*, ROM 44656, 80.0 [M]; *C. nigripinnis*, ROM 884CS, 2: 55.0–90.0 [CS]; *Diploprion bifasciatus*, ROM 39058, 64.0 [CS]; *Epinephelus merra*, ROM 845CS, 3: 71.4–95.0 [CS], ROM 44635, 2: 112.6–117.2 [M], ROM 44586, 77.0 [M]; *Grammistes ocellatus*, ROM 53527, 93.0 [CS]; *G. sexlineatus*, ROM 37769CS, 32.9 [CS]; *Hemanthias vivanus*, ROM 41451, 44.0 [CS]; *Holanthias martinicensis*, ROM 36931, 29.5 [CS]; *Liopropoma susumi*, ROM 1348CS, 52.6 [CS]; *Nemanthias carberryi*, ROM 1349CS, 4: 39.4–44.3 [CS], ROM 43468, 2: 56.5–64.0 [M]; *Plectranthias longimanus*, ROM 55093, 27.0 [CS]; *Pseudanthias* sp., ROM 775CS, 4: 52.0–58.0 [CS]; *Pseudogramma polyacantha*, AMS I.24548-004, 2: 11.9–13.8 [CS], AMS I.23764-004, 2: 8.4–11.6 [CS], AMS I. 20948-011, 3.4 [CS], AMS I.23764-004, 2.7 [CS], ROM 867CS, 5: 15.6–33.1 [CS], ROM 1340CS, 6: 11.5–18.0 [CS], ROM 1341CS, 2: 12.0–12.8 [CS], ROM 1342CS, 11.7 [CS], ROM 1343CS, 2: 15.3–18.8 [CS]; *Rainfordia opercularis*, ROM 39059, 64.3 [X]; *Rypticus saponaceus*,

ROM 39095, 72.0 [M]; *Serranus tigrinus*, 1345CS, 33.0 [CS]; *Suttonia lineata*, ROM 53532, 51.1 [X].

AN OVERVIEW OF THE PLESIOPIDAE

Genera of the Plesiopidae.—Seven genera are currently included in the family Plesiopidae: *Assessor*, *Calloplesiops*, *Fraudella*, *Paraplesiops*, *Plesiops*, *Steeneichthys*, and *Trachinops*. *Plesiops* was the first to be described (Cuvier, 1816). Its species exhibit the largest size variation as adults, from 60 to 200 mm SL. They are generally dark-bodied fishes, often with colored stripes on the dorsal and anal fins. They have long pelvic fins and deeply incised membranes between the spines of the dorsal fin. The genus is found on shallow tropical and subtropical reefs from the east African coast and the Red Sea, across the Indian Ocean, through Indonesia and into the western Pacific as far east as the Cook Islands. *Plesiops* has not been reviewed since Inger (1955), and problems with its alpha systematics have been recognized for some time. For example, Hoese and Kuitert (1984: 8) pointed out that “there are difficulties identifying some Australian species.” This has been partially rectified by Mooi and Randall (1991) who described three additional Australian species, increasing the number of nominal species to 10. A revision of the genus will be published elsewhere.

Paraplesiops, *Trachinops*, and *Fraudella* are restricted to Australian coasts. The first is superficially similar to *Plesiops*, although it is often more spectacularly colored. Hoese and Kuitert (1984) and Hutchins (1987) described five species in this genus. The latter author also discussed Quaternary glacial events as factors influencing the current distribution of these cryptic, cave-dwelling species of rocky and coral reefs. *Trachinops* looks superficially like a pseudochromid (and one was described as such by Johnston, 1902), as they are elongate, colorful, and small (<60 mm SL). They differ from the pseudochromids, and other plesiopids, in having an elongate dorsal fin with numerous spinous elements and in having elongate central caudal rays produced to form a filament. The species are found in schools on shallow rocky reefs of temperate Australia. A revision describing four species was provided by Allen (1977). The monotypic *Fraudella* is the least known of the plesiopid genera; it is found only off the Queensland coast. It is rare in collections, perhaps because it occurs at depths beyond those of most ichthyoclide collections. One specimen was taken from a sponge dredged from 40 m (Whitley, 1935). It was originally placed in the Hypoplectrididae (=Serranidae) by Whitley (1935) after he mistakenly reported 1,5 pelvic-fin rays, although he recognized its similarity to *Paraplesiops*. Böhlke (1960) considered it a member of the Grammatidae. After re-examination of the type material, Hoese and Kuitert (1984) assigned *Fraudella* to the Plesiopidae.

Assessor comprises three species (Allen and Kuitert, 1976). They commonly form aggregations of more than 100 individuals in caves or crevices, always in areas of subdued light. In at least one of the species males orally incubate the eggs. All species occur on coral reefs, one in the Ryukyu Islands and Taiwan, and two off the Great Barrier Reef and neighboring seas.

Calloplesiops is a spectacularly colored monotypic genus that is much sought after in the aquarium trade. With its black body with white spots and large ocellus on the posterior rays of the dorsal fin, it has been suggested to mimic the head of a moray eel (McCosker, 1977). This wide-ranging species of the Indo-west Pacific has been described independently on numerous occasions (McCosker, 1978). There has been some suggestion that two species should be recognized (Condé, 1983).

Steeneichthys was first described by Allen and Randall (1985), and a second

species has since been added (Allen, 1987). They are tiny fishes, with a maximum size of only 30 mm SL, that range from American Samoa to the eastern Indian Ocean.

Other genera have at times been assigned to the family Plesiopidae. *Acanthoclinus*, *Acanthoplesiops*, and *Belonepterygion*, currently regarded as members of the family Acanthoclinidae, were at one time included as plesiopids, the first two by Regan (1913) and the third by Jordan (1923). Jordan (1923) also included *Tosana* Smith and Pope, a genus now placed in the Anthiinae (Serranidae). Fowler (1938: 142) referred his new genus *Nannapogon* "with some hesitancy to the Plesiopidae"; it has since been identified as a pomacentrid (Randall, 1973). Kottaus (1976) assigned his new genus *Parabarossia* to the Plesiopidae, but it is apparently a synonym for *Grammatonotus* (family Callanthiidae) (Springer, 1982; Eschmeyer and Bailey, 1990).

Historical Review of Plesiopid Classification. — Cuvier (1816) originally placed the genus *Plesiops* in his Labroides nearest to taxa now considered members of the Pomacentridae. The Labroides included some labroids as defined by Kaufman and Liem (1982). Rüppell (1835) followed this arrangement, placing *Plesiops* near *Labrus*, and Richardson (1836) assigned *Plesiops* to his family Labroideae. A similar relationship was retained by Swainson (1839), who placed the genus in the subfamily Labrinae of his family Chaetodonidae. Müller and Troschel (1849) created a new family, the Pseudochromidae, which included true pseudochromids and *Plesiops*, but continued to compare it to labroid taxa, as well as including the genus *Nandus* as a possible relative.

Günther (1861) assigned *Plesiops* and a new genus *Trachinops* to the Plesiopina, one of three groups in a new family, the Nandidae. None of the genera he included in the other two groups are currently considered related to his Plesiopina, and the composition of Nandidae itself has been altered (Nelson, 1984). In 1875, Bleeker resurrected the concept of a large family "Pseudochromidoides" consisting of three groups: 1) Cichlopsini for *Cichlops* (now *Labricinus*), *Gramma* (now in Grammatidae), *Pseudochromis*, *Pseudogramma* (now a serranid), and Günther's *Trachinops*; 2) Pseudoplesiopini for *Pseudoplesiops*; and 3) Plesiopini for *Plesiops* and a new genus *Paraplesiops*. Bleeker did maintain a family Nandidae as a neighboring taxon. Boulenger (1895) radically altered and complicated the classification by placing *Plesiops*, *Paraplesiops*, and *Pseudoplesiops* near *Callanthias* [now in the Callanthiidae (Anderson and Johnson, 1984; Johnson, 1984)] in the subfamily Serranina of his Serranidae. Boulenger (1895) regarded the remaining genera of Bleeker's Pseudochromidoides as closely allied to the serranids and connected with them through *Plesiops* and its allies.

Regan (1913) introduced the Plesiopidae as a distinct family, and he included the genera *Plesiops*, *Paraplesiops*, *Trachinops*, *Acanthoclinus*, and *Acanthoplesiops*. The latter two genera were previously considered either as a separate family, the Acanthoclinidae (Günther, 1861), or as blennioids (see Systematic Remarks in Hardy, 1985). Jordan (1923) recognized the Plesiopidae and Acanthoclinidae as separate families, although he considered them closely related to the Pseudoplesiopidae and Pseudochromidae. He further suggested that these four families were allied to the serranid subfamily Anthiinae. Weber and de Beaufort (1929) concurred that the Plesiopidae and Acanthoclinidae each deserved familial status. This status has prevailed to the present (Böhlke, 1960; Greenwood et al., 1966; Gosline, 1968, 1971; Nelson, 1984; Johnson, 1984), not because it has been corroborated by phylogenetic evidence, but because there has been no evidence provided to justify a change.

Plesiopid and Acanthoclinid Relationships: Previous Views. — Boulenger (1895) was the first to consider the Plesiopidae as a near relative of the serranids. Regan (1912, 1913) followed this lead, but included the then known acanthoclinid taxa with the plesiopids on the basis of a reduced number of pelvic-fin rays with the first soft ray being only bifid (as opposed to having multiple branches). Jordan (1923), as discussed above, recognized the Plesiopidae and Acanthoclinidae as distinct families, but curiously related them to the Anthiinae, hence proposing what would today be termed a paraphyletic Serranidae. Since then, acanthoclinids and plesiopids have been placed as basal members of the suborder Percoidei near the serranids, although no justification for such an arrangement, other than general similarity, has ever been made.

Gosline (1960), while investigating relationships of the Grammistidae [now Grammistini of the Serranidae (Johnson, 1983)], was one of the first to look at internal characters of *Plesiops*. He identified some possibly unique features, including a prominent cleithral hook and an open sensory canal on the preopercle, but concluded that, of the taxa he examined, "*Plesiops* appears hardest to define on the basis of internal features" (p. 34).

Böhlke (1960) attempted to define the families of serranoid fishes with disjunct lateral lines. These are a diverse assemblage that all have specialized conditions of the lateral line, including interrupted, posteriorly incomplete, multiple, and completely absent. He included seven families: Pseudochromidae, Pseudoplesiopidae, Anisochromidae, Plesiopidae, Acanthoclinidae, Pseudogrammididae, and Grammatidae. At the dawn of phylogenetic studies of percoids, the first three families were recognized as monophyletic by Springer et al. (1977), and combined under the Pseudochromidae. The Pseudogrammididae have since been recognized as epinepheline serranids (Johnson, 1983). The Grammatidae also have been redefined to include only *Gramma* and *Lipogramma* (Johnson, 1984). Of the remaining genera that Böhlke (1960) included in this family, *Fraudella* has been placed in the Plesiopidae (Hoesé and Kuitert, 1984), *Pseudochromichthys* is regarded as a synonym of *Plesiops* (Inger, 1955), and *Grammatonotus* and *Stigmatonotus*, identified as a callanthiid and a serranid respectively (Johnson, 1984), have been removed from the original subset of taxa entirely.

Springer et al. (1977) pointed out that some families with disjunct lateral lines, such as the Opistognathidae, were overlooked by Böhlke (1960) and should be included within this subset. These taxa, other than the unusual condition of the lateral line, share the presence of five or six branchiostegals (primitively seven in percoids), anterior and posterior ceratohyals sutured together, and hypurals fused in a 1+2 and 3+4 arrangement, with the latter being fused to the urostylar complex as well. However, these characters are not unique to these fishes, and are found in the same combination in most blennioids (sensu George and Springer, 1980), pholidichthyids, and notographtids (Gill, 1990). Since that time, Godkin and Winterbottom (1985) placed the Congrogadidae as a derived subfamily within the Pseudochromidae. Earlier, Gosline (1968) had suggested a close relationship between the Acanthoclinidae and Opistognathidae, but had also postulated that they, along with the Plesiopidae, were primitive members of a basal blennioid stock. There has been little evidence identified to support such a relationship. During an attempt at a species-level phylogeny of the Acanthoclinidae, Hardy (1985) was unable to suggest a sister group.

Most recently, Mok et al. (1990) proposed that the Plesiopidae and Acanthoclinidae are sister groups, and that these together were the sister group of the Pseudochromidae, Opistognathidae, and Grammatidae. Within this latter group, the Opistognathidae and Grammatidae are most closely related. However, his

cladogram is based on few characters, and I concur with Smith-Vaniz and Johnson's (1990) evaluation that these are either invalid or have been misinterpreted. Mok et al.'s (1990) study was superficial (few taxa of each family examined), and many of the polarity decisions are confused or equivocal. No one has yet established that these five families, Plesiopidae, Acanthoclinidae, Pseudochromidae, Grammatidae, and Opistognathidae—the “pseudochromoids” sensu Mooi (1990)—actually form a monophyletic group. Relationships of these taxa based on careful and reasonable analysis remain to be hypothesized.

PHYLOGENY OF THE PLESIOPIDAE

An earlier search for a plesiopid outgroup using a non-traditional character suite, egg surface morphology, was unsuccessful (Mooi, 1990). However, some of the examined features established similarities between egg types of the acanthoclinids and some plesiopids, and indicated that at least some genera of plesiopids have strikingly similar and perhaps unique chorionic structures (Mooi, 1990). These results suggested that the Acanthoclinidae might be more closely related to the Plesiopidae than to other pseudochromoids and provided a starting point for investigating plesiopid phylogeny. I used the Acanthoclinidae as a first outgroup (sister group), and, accepting the hypotheses of Johnson (1984) as a best estimate of relationships, employed the remaining pseudochromoids (Pseudochromidae, Grammatidae, and Opistognathidae) as a composite second outgroup. Recent phylogenies of the acanthoclinids by Smith-Vaniz and Johnson (1990) and of the pseudochromids by Gill (1990) have helped to identify basal genera within these families. This has facilitated outgroup comparison by providing a minimum number of taxa required to complete a survey of character state distributions. I also examined other basal percoid taxa of the Serranidae, Moronidae, and Callanthiidae, as well as representatives of a few “higher” percoids (see Material Examined). Unless this series of composite outgroups is itself a monophyletic sister group to the plesiopids, which is highly unlikely, such a comparison permits the identification of autapomorphies that define the family Plesiopidae.

As is necessary with a phylogenetic analysis, I initially assumed the Plesiopidae to be monophyletic. However, many characters that appeared derived for the family with respect to other lower percoid families were consistently shared with the Acanthoclinidae. Although originally reluctant to do so, I came to the conclusion that the shared features of plesiopids and acanthoclinids would be most parsimoniously explained by considering the two families together as members of the ingroup. This greatly facilitated the analysis, as I then had (I believe) a monophyletic rather than paraphyletic ingroup with which to work. Following my recommendation based on these preliminary results, Smith-Vaniz and Johnson (1990) synonymized the Acanthoclinidae (sensu Hardy, 1985) with the Plesiopidae (sensu Hoese and Kuitert, 1984). Both the Acanthoclinidae and Plesiopidae (as Plesiopina) were erected as suprageneric taxa by Günther (1861: 297 and 362, respectively). Although the name Acanthoclinidae has page priority, Smith-Vaniz and Johnson (1990), as first revisers, have elected to use the name Plesiopidae, and “acanthoclinids” have been included as a subfamily within this expanded family on my advice. I follow this decision here, and for the remainder of the paper, use the name Plesiopidae (or plesiopid) and Acanthoclininae (or acanthoclinine) in the sense of Smith-Vaniz and Johnson (1990), except where noted. Smith-Vaniz and Johnson (1990: 220) also suggested that the Notograptidae might be related to acanthoclinines; this possible affinity is explored elsewhere (Gill and Mooi, 1992).

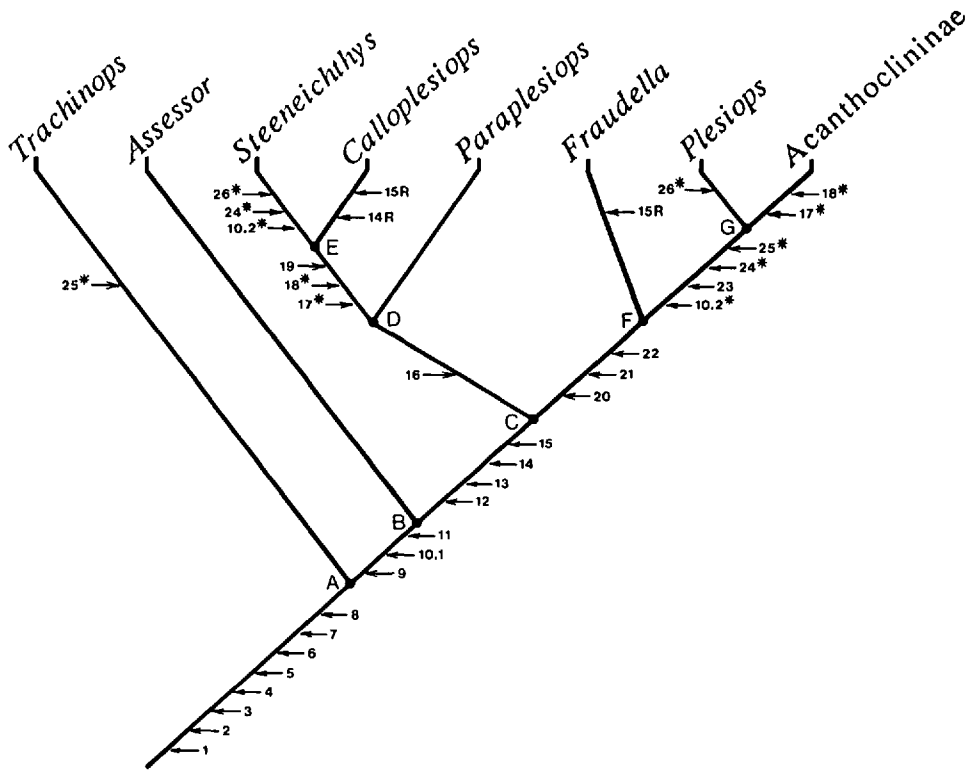


Figure 1. Cladogram of the family Plesiopidae. Nodes are lettered. Numbers directly below each node are characters supporting that node. Characters marked by asterisks are homoplastic, those by "R" are apparent reversals to a condition similar to the plesiomorphic state. Node letter and character number identify the character in the text. See text for autapomorphies of terminal taxa and character descriptions.

Character Analysis.—The character notation follows that of Figure 1. Each node of the cladogram is assigned a letter. Characters are assigned a number and are found below the node to which they refer. Homoplastic characters are indicated by asterisks and appear below each node where the homoplasy is evident; characters with apparent reversals to a condition similar to that of the plesiomorphic state are marked by "R." Characters considered to be composed of more than one derived state, i.e., transformation series, have sequential states in the series given a secondary number (e.g., if character 3 has 2 derived states in sequence, these are 3.1 and 3.2). This numbering maintains character transformation integrity for those interested in character state evolution, and allows nodal support to be easily identified. The monophyly of terminal taxa is discussed at the node from which the taxon originates after the characters supporting that node have been described.

NODE A: Characters 1–8

1. Posterior Subpelvic Concavity Present

Plesiomorphy.—In all outgroup taxa examined, the ventral surface of the pelvic girdle posterior to the subpelvic processes is flat or only slightly concave (Fig. 2a).

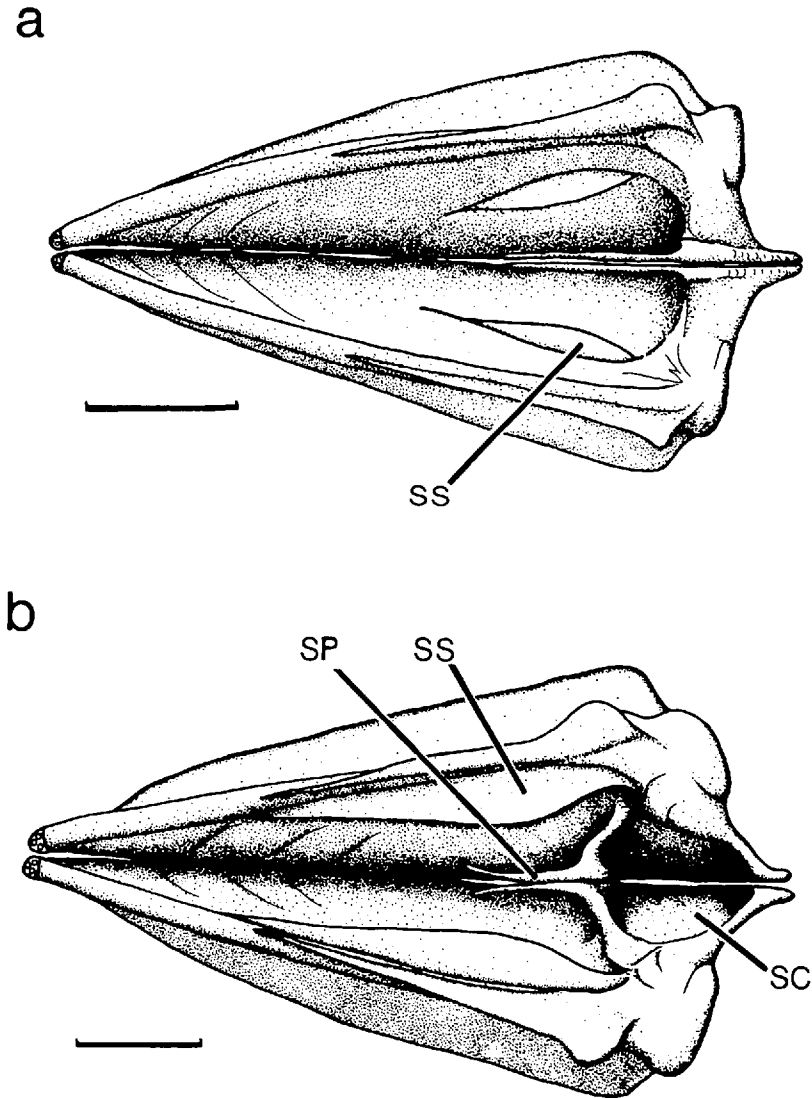


Figure 2. Ventral views of the pelvic girdles of: a) *Gramma loreto* [ROM 997CS, 39.6 mm]; b) *Callopleles altivelis* [ROM 894CS, 50.0 mm]. Spines and segmented rays removed. Anterior to left. SC = subpelvic concavity, SP = subpelvic process, SS = subpelvic shelf. Scale bars are 1 mm.

Apomorphy.—All taxa above Node A have a deeply concave area just posterior to the subpelvic processes (Fig. 2b). This appears to be an area for increased muscle attachment for the abductor superficialis pelvici and abductor profundus pelvici.

Homoplasy.—None.

2. Subpelvic Shelf Present

Plesiomorphy.—Outgroups do not have a wide shelf projecting from the ventral surface of the main strut of the basipterygium. The ventral surface of the basip-

terygium is generally smooth and without projections other than the subpelvic processes, except for *Gramma* (Fig. 2a) and some pseudochromids as noted below.

Apomorphy.—Plesiopids have a shelf projecting medially from the ventral surface of the main strut of the basipterygium (Fig. 2b). This shelf provides a surface for muscle attachment; its ventral surface for the arrector ventralis pelvici and its dorsal surface for the abductor profundus pelvici.

Homoplasies.—None. Both *Gramma* and some pseudochromids have a ridge or shelf on the ventral surface of the basipterygium, but these arise from a medial region of the pelvic girdle rather than from the main lateral strut (Fig. 2a). I interpret this difference as a nonhomologous condition. *Callanthias* has a wide subpelvic shelf, but it does not originate from the strut over its entire length; *Grammatonotus*, its potential sister group (Johnson, 1984), has a subpelvic shelf very similar to that of *Gramma* and pseudochromids. At least some members of the Anthiinae (Serranidae) have a structure very similar to that of plesiopids, but this subfamily is otherwise too distantly related to suggest homology.

3. Reduction to Four or Fewer Segmented Pelvic-fin Rays

Plesiomorphy.—All outgroups have, at least primitively, five segmented pelvic-fin rays.

Apomorphy.—Plesiopids have only four segmented pelvic-fin rays, further reduced to two in acanthoclinines.

Homoplasies.—Pseudochromids show a trend of reduction in number of segmented pelvic-fin rays in more derived taxa. Böhlke (1960: 6) concluded from his studies on serranoids with disjunct lateral lines that "the loss of one or several ventral rays may not be as significant a step as previously thought." This being said, current views of relationships of taxa examined here limits reductions in pelvic ray number to the derived pseudochromids and the plesiopids. With this limitation, parallelisms are reduced and perhaps more weight can be given to such reductions.

Remarks.—Johnson (1992) has shown that homology of the medial pelvic-fin ray can sometimes be determined by evidence of fusion with the middle radial in the form of cartilage on the tip of the ray at some point in ontogeny. Although the shape of the medial ray of most plesiopids is consistent with such fusion (Character 14), I am unable to find evidence of cartilage that would indicate this more conclusively. Homology of the remaining rays thus remains impossible to ascertain at this time. For other characters involving ray homology, I have assumed (perhaps incorrectly) that members of the Plesiopidae have lost the medial (5th) ray, retaining rays 1 to 4. In acanthoclinines, where even more rays have been lost, the remaining rays are considered homologous with lateral rays of other plesiopids.

4. Extensor Proprius Pelvici Inserts onto 2nd Segmented Pelvic-fin Ray

Plesiomorphy.—The extensor proprius pelvici usually inserts onto one or two of the innermost rays of the pelvic fin (Winterbottom, 1974). This is true of the majority of the outgroups. *Morone* and *Epinephelus* have the muscle only inserting onto the 5th segmented ray, and in *Opistognathus* and basal pseudochromids it

inserts onto the 4th and 5th segmented rays (perhaps also the 3rd in pseudochromids). *Gramma* has the 3rd, 4th, and 5th rays involved.

Apomorphy.—In plesiopids, the extensor proprius inserts onto the 2nd, 3rd, and 4th segmented pelvic-fin rays. I know of no other taxon where this muscle inserts onto the 2nd ray. Acanthoclinines are considered further derived in that the extensor proprius muscle is absent (see Remarks).

Homoplasy.—None.

Remarks.—With the assumption that plesiopids have lost the 5th segmented pelvic-fin ray, it is possible that the extensor proprius has merely shifted its insertions onto the remaining rays from a primitive condition of inserting onto the 3rd, 4th, and 5th segmented rays. In this scenario, the muscle insertion onto the 2nd ray would not be an independent event, but would be linked to loss of the 5th ray. Evidence for such a linkage might be discovered by investigating the condition of the extensor proprius in the Pseudochromidae where there is a reduction in number of segmented pelvic-fin rays in more derived taxa. Acanthoclinines have a greatly reduced number of pelvic-fin rays (to only 2), and have lost the extensor proprius entirely.

5. *Distal Radial of Each Dorsal Spine-bearing Pterygiophore (Except Last Fused to Following Pterygiophore to Form a Fully Interlocking Bony Ring-shaped Articulation with the Spine)*

Plesiomorphy.—In outgroups, the dorsal spine-bearing pterygiophores are quite close together and each is composed of two elements. The large proximal element is the product of the fusion of a proximal radial and a middle radial, and the smaller free distal element is the distal radial. The distal radial usually articulates with both its serially associated and secondarily associated proximal-middle elements (Fig. 3a). It also bears a small hook that articulates with the serially associated spine. The proximal-middle element also often bears a process for articulation with its secondarily associated spine.

Apomorphy.—The plesiopids have dorsal spine-bearing pterygiophores that are quite widely spaced and each is a single element. They are composed of a distal radial that has lost the articulation with its serially associated proximal-middle radial and has completely fused to its secondarily associated proximal-middle radial. The result is a single unit with a closed bony ring that interlocks with the articulating spine (Fig. 3b).

Homoplasies.—The genus *Pseudogramma* of the Grammistini, a tribe of the Epinephelinae (Serranidae), has similar closed rings that interlock with spines. The distal radial portion, however, is robust and block-like, not fine and delicate as in the Plesiopidae. Furthermore, *Pseudogramma* appears to have the most derived condition of a series of gradual changes in pterygiophore morphology within the grammistins (pers. obs.; C. Baldwin and D. Johnson, pers. comm.). Grammistins are well-defined by numerous autapomorphies not shared by plesiopids. This, and the difference in distal pterygiophore shape, rules out homology of these similar pterygiophore morphologies.

Notograptus also has closed pterygiophores, as do some blennioids and labroids, all presumably developed in a similar manner as in *Pseudogramma* and plesiopids, with fusion of the distal radial to its secondarily associated proximal-middle radial. The phylogenetic relationships of *Notograptus* are enigmatic. Gosline (1968) suggested a relationship with congrogadines and placed them in a blennioid-trachi-

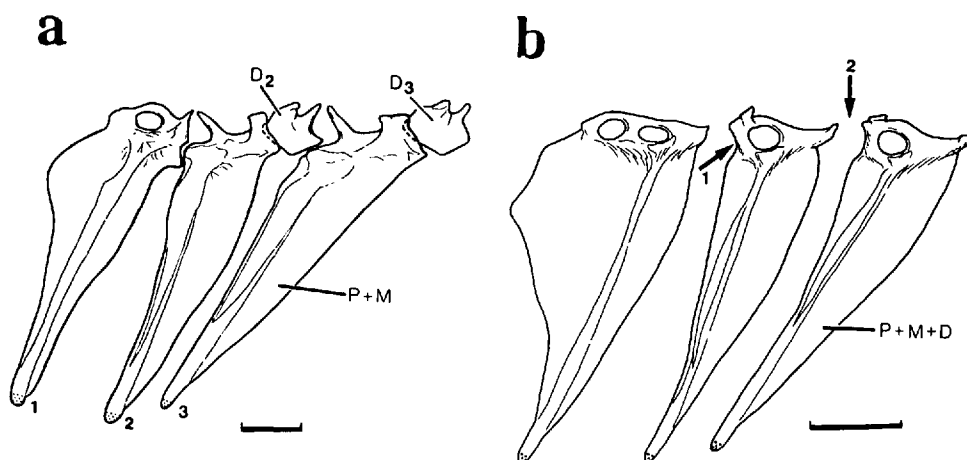


Figure 3. First three dorsal-fin spine-bearing pterygiophores of: a) *Epinephelus merra* [ROM 845CS, 71.4 mm], D_2 = distal radial serially associated with pterygiophore 2 and secondarily associated with pterygiophore 3, D_3 = distal pterygiophore serially associated with pterygiophore 3, $P + M$ = proximal-middle radial, dotted lines show outline of distal radials in articulating groove of serially associated proximal-middle radial (first distal radial is assumed lost or fused to the first proximal-middle radial); b) *Callopleksiops altivelis* [ROM 894CS, 50.0 mm], $P + M + D$ = proximal-middle-distal radial, arrows point to fusion of secondarily associated distal with proximal-middle element (1) and loss of articulation between distal and serially associated proximal-middle element (2). Anterior to left. In both, spines removed; stippling represents cartilage. Scale bars are 1 mm.

noid assemblage. Godkin and Winterbottom (1985) showed that congrogadines are pseudochromids, and discounted a possible congrogadine-*Notograptus* relationship. It is possible that *Notograptus* belongs with the plesiopids, but a more detailed study of *Notograptus* is necessary before its affinities can be resolved (Gill and Mooi, 1993).

Mok et al. (1990) implied homology between the spinous pterygiophore condition in grammistins, plesiopids, acanthoclinids (sensu Hardy, 1985), and opistognathids based on a misinterpretation of the morphology. They believed that the distal radials were lacking in these groups. This is clearly incorrect for grammistins, plesiopids, and acanthoclinids. An ontogenetic sequence of pterygiophore development in *Pseudogramma* clearly shows the development of distal radials and their eventual fusion with the proximal-middle radial (Fig. 4). This is also evident in *Plesiops* (Fig. 5). However, the distal radials are missing in opistognathids and *Lipogramma* (a genus of Grammatidae not examined by Mok et al., 1990) (Fig. 6). Apparently these elements never form during ontogeny. As the distal radials are the last pterygiophore element to develop in *Pseudogramma* (Fig. 4a), I propose that the absence of distals is a paedomorphic condition. *Gramma*, the apparent sister group to *Lipogramma*, has distal radials. *Lipogramma* is considerably smaller than *Gramma*, and the retention of a juvenile character and reduction in body size suggest that the genus is progenetic, if the loss of distal radials is due to developmental truncation and if small size is derived. The condition in Opistognathidae is likely to be nonhomologous to that of *Lipogramma* (no evidence for relationship currently exists, but see Gill and Mooi, this volume), and could be the result of any of the three recognized developmental models of paedomorphism (McNamara, 1986). Indeed, many opistognathid characters might be interpreted as paedomorphic morphologies, although a phylogeny and knowledge of ontogenetic trajectories of characters are required to make this statement

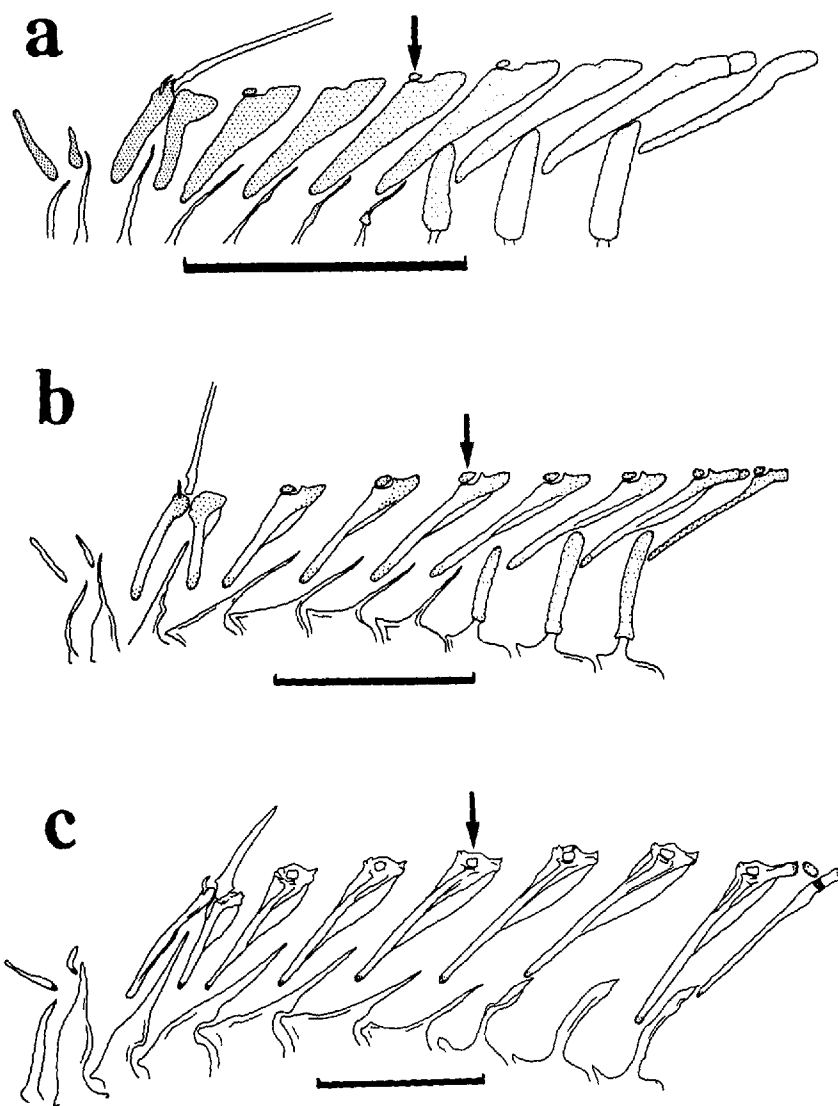


Figure 4. Development of the dorsal-fin spine-bearing pterygiophores of *Pseudogramma polyacantha*: a) 8.4 mm [AMS I.23764-004CS], arrow indicates free distal radial, note not all distals have yet formed; b) 11.6 mm [AMS I.23598-025CS], arrow indicates free distal radial, but all distal radials have now formed; c) 14.9 mm [ROM 1340CS], arrow indicates complete fusion of distal radial with secondarily associated proximal-middle element. All but first two dorsal spines removed in each. Tips of neural spines shown between pterygiophores. First two free elements are supraneurals (predorsals); last element is pterygiophore of first segmented ray. Stippling represents cartilage. Anterior to left. Scale bars are 1 mm.

with any certainty. However, if paedomorphism is a common phenomenon in opistognathid development, this might explain the difficulty in discovering its relationships. Paedomorphosis can confuse a phylogenetic analysis unless there is a sufficient number of characters that are not developmentally truncated (Fink, 1982; Mooi, 1987).

Remarks.—The morphology of the spine-bearing pterygiophores of *Paraplesiops*

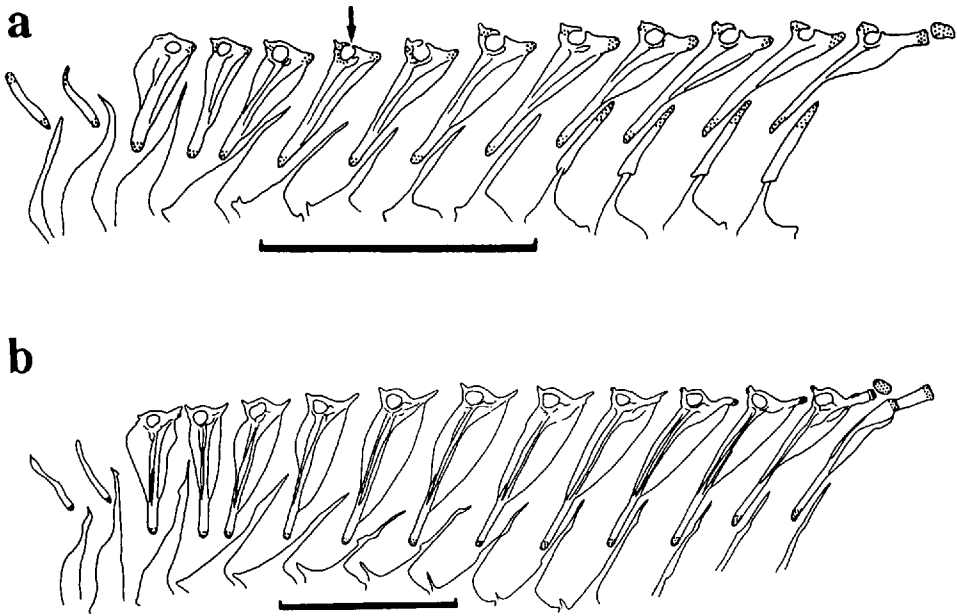


Figure 5. Development of dorsal-fin spine-bearing pterygiophores of *Plesiops coeruleolineatus*: a) 9.3 mm [ANSP 108721CS], arrow indicates most anterior pterygiophore with an incomplete bony ring; b) 12.6 mm [ROM 1337CS], note that all pterygiophores have complete bony rings. Spines removed; neural spines shown between pterygiophores. First two free elements are supraneurals (predorsals). Stippling represents cartilage. Anterior to left. Scale bars are 1 mm.

is intriguing. Most members of the genus have what appears to be a primitive condition where the distal radial is autogenous and articulates with both its serially associated element and its secondarily associated element (Fig. 7a). These still appear relatively derived compared to the outgroups because of the modified and narrowed articulation of the distal radial with the secondarily associated proximal-middle radial. One species, *Paraplesiops alisonae*, seems intermediate between other *Paraplesiops* species and remaining plesiopids. The distal radials of the spinous pterygiophores of *P. alisonae* have lost their articulation with their serially associated proximal-middle radials (a derived condition), but at least one anterior distal (occasionally more) remains freely articulating with the secondarily associated proximal-middle radial (a primitive condition) (Fig. 7b). Subsequent posterior distals are only fused basally to the secondarily associated proximal-middle radials, but further posteriorly the distals fuse completely with these elements to form a bony ring (Fig. 7b). This suggests a transformation series from the primitive outgroup condition to the relatively primitive state of most *Paraplesiops* species, which then is modified to form the intermediate *P. alisonae* condition, culminating in a fully fused interlocking mechanism of the remaining plesiopids (Fig. 8). With this interpretation, *Paraplesiops* is not a monophyletic group. However, I have examined the ontogeny of this feature, and it suggests a different scenario. In *Plesiops*, the only genus for which I have a series of juveniles, it is apparent that it is the base of the distal radial that first fuses to the proximal-middle element. The dorsal process then fuses to form the closed bony ring. The fusion of these elements occurs in an anterior to posterior direction, so that the distal radials of the anterior pterygiophores are fully fused when the more posterior distal radials are only fused basally and the ring is not yet closed (Fig. 5a). Indirect evidence

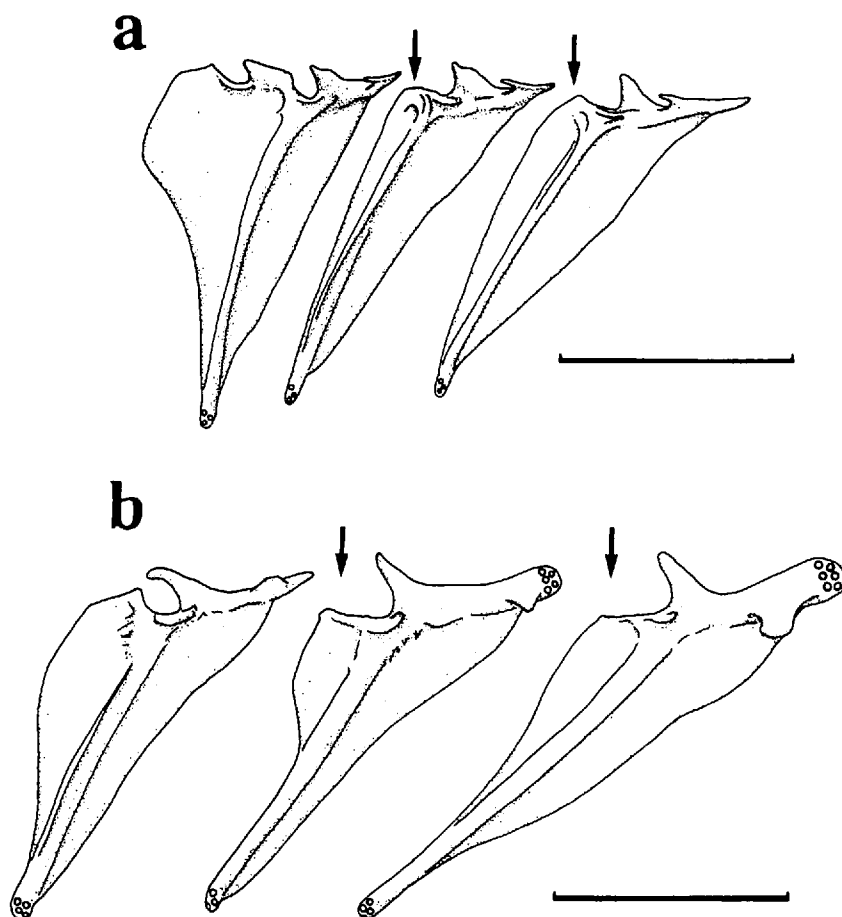


Figure 6. Anterior three dorsal-fin pterygiophores of: a) *Lipogramma klayi* [ANSP 127671CS, 23.8 mm]; b) *Opistognathus* sp. [ROM 778CS, 54.0 mm], distance between pterygiophores reduced. Arrows indicate where distal radials would normally be if they formed. Open circles represent cartilage. Anterior to left. Scale bars are 1 mm.

of this occurring in other plesiopids is found in some individuals of *Trachinops noarlungae* where some of the posterior spinous pterygiophores do not have closed bony rings even in adults. Such an ontogeny is in direct contrast with the observed adult condition in *Paraplesiops alisonae* where it is the anterior pterygiophores that are not fully fused (Fig. 7b). I interpret this as meaning that *Paraplesiops* has developed an alternate and derived developmental pathway that is nonhomologous with that of other plesiopids. This interpretation is secondarily supported by other characters that place *Paraplesiops* deeply within the phylogeny of the group. The ontogenetic evidence, then, suggests that the initial polarization of the feature as shown in Figure 8 is incorrect. Using FIG/FOG comparison, I have reinterpreted the character evolution (Fig. 9). Within plesiopids, the fully fused distal and bony ring is a primitive state; *Paraplesiops alisonae* occupies an intermediate position where a new developmental pathway has been derived in which anterior distal radials do not fuse completely, and other members of *Paraplesiops* are united by a secondarily derived condition of distal radials that articulate with

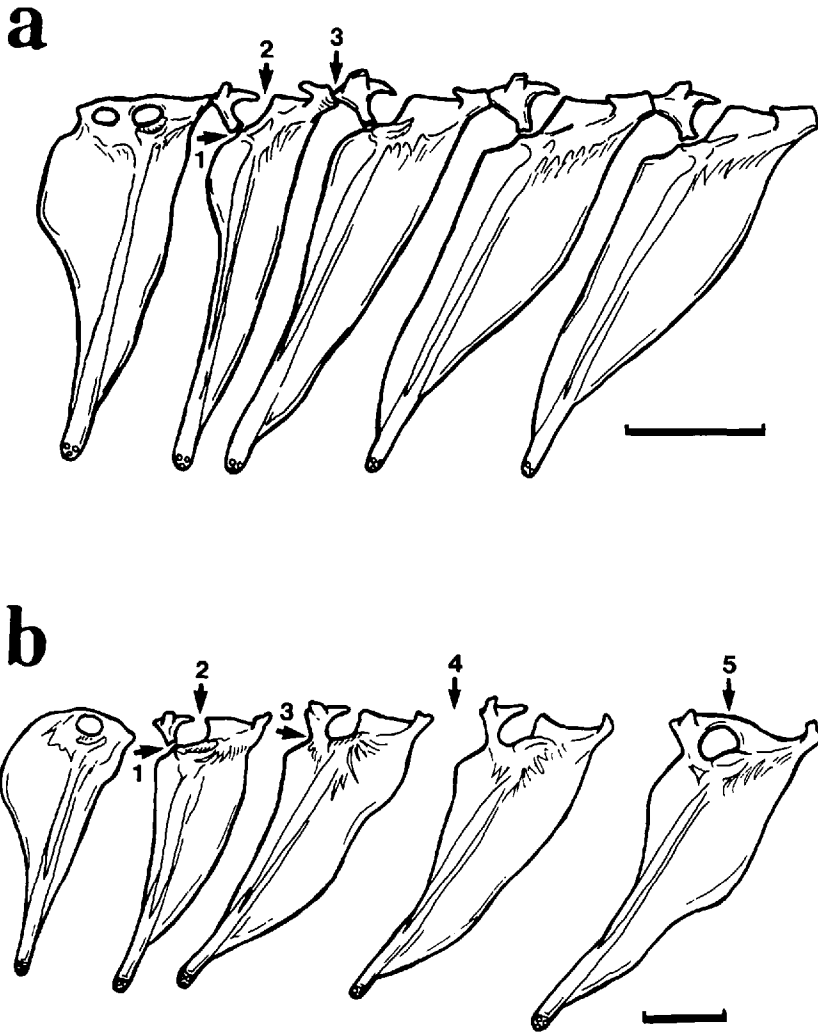


Figure 7. Anterior five dorsal-fin pterygiophores of *Paraplesiops*: a) *P. poweri* [USNM 274578CS, 47.8 mm], arrow 1 shows articulation of the distal radial with its secondarily associated pterygiophore, arrow 2 indicates the lack of fusion dorsally between the distal radial and the secondarily associated proximal-middle radial, and arrow 3 notes the articulation of the distal radial with its serially associated pterygiophore; b) *P. alisonae* [NMV A2259CS, 64.5 mm], arrow 1 shows articulation of anterior distal radial with its secondarily associated pterygiophore, arrow 2 indicates lack of fusion dorsally between anterior distal radial and the proximal-middle radial, arrow 3 indicates fusion of further posterior distal radial with the proximal-middle element of its secondarily associated pterygiophore, arrow 4 notes the loss of articulation of the distal radial with its serially associated pterygiophore, arrow 5 shows dorsal fusion of the distal radial with the secondarily associated proximal-middle radial to form a bony ring in more posterior pterygiophores. Small open circles represent cartilage. Anterior to left. Scale bars are 1 mm.

both the serially and secondarily associated proximal-middle radials. The new developmental pathway is an autapomorphy for the genus *Paraplesiops*.

A reviewer suggested that the condition in *Paraplesiops alisonae* might not be intermediate, but could instead be derived from the condition in remaining members of its genus, particularly if the developmental pathway is taken to be com-

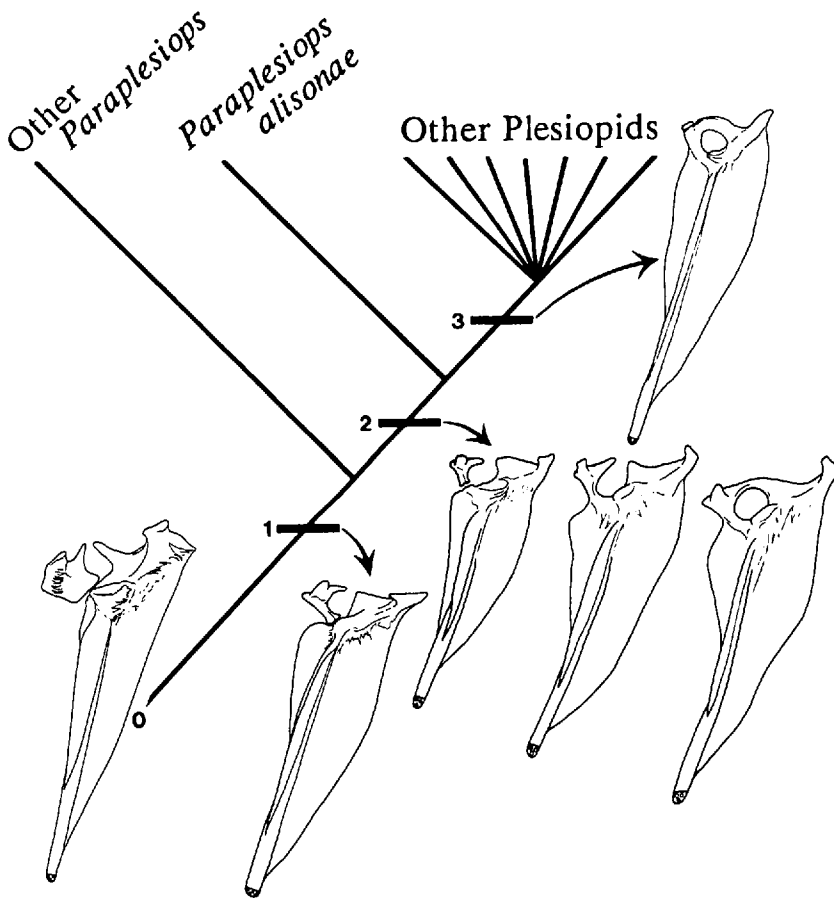


Figure 8. Initial scenario for pterygiophore evolution in the Plesiopidae. 0 = primitive condition of distal radials articulating with both serially and secondarily associated proximal-middle radials; 1 = initial modification to a specialized articulation of the distal radial with the secondarily associated pterygiophore as exemplified by most *Paraplesiops* species; 2 = intermediate condition of anterior distal radials with typical *Paraplesiops* state and subsequent posterior distal radials with ventral fusion and then dorsal fusion to complete a bony ring (*P. alisonae*); 3 = culmination of transformation series to all spine-bearing dorsal-fin pterygiophores with complete bony ring.

pletely novel. This is possible, but considering the position of *Paraplesiops* within the Plesiopidae, it seems more parsimonious that some features of pterygiophore development of a common ancestor have been retained and modified, as opposed to the introduction of an entirely novel pathway. However the details of pterygiophore evolution within *Paraplesiops* are resolved, it remains a reasonable hypothesis that the pterygiophore morphology of the genus is autapomorphic.

6. Parasphenoid Keel Present

Plesiomorphy.—Primitively, the parasphenoid is smooth mid-ventrally.

Apomorphy.—All plesiopids have a mid-ventral keel on the parasphenoid. This blade-like ridge is situated posteriorly on the parasphenoid and divides anteriorly to meet the lateral edges of the bone (Fig. 10). The ridge is less pronounced in

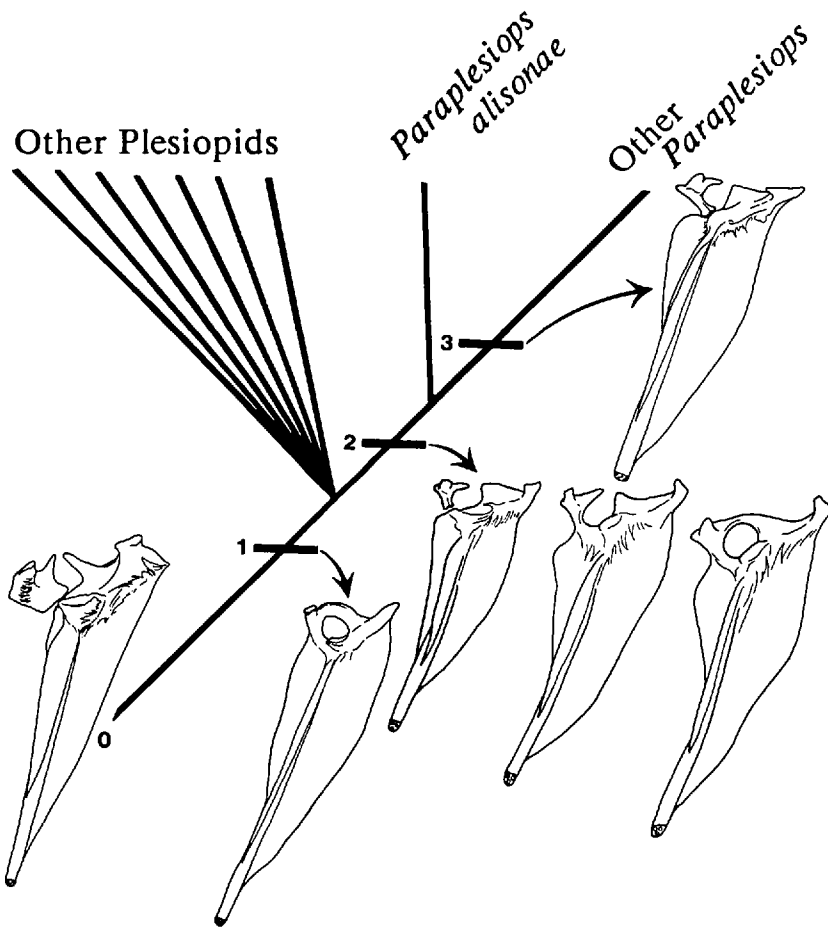


Figure 9. Modified scenario of pterygiophore evolution in the Plesiopidae. 0 = primitive condition of distal radials articulating with both serially and secondarily associated pterygiophores; 1 = initial modification with distal radial fully fused with secondarily associated pterygiophore; 2 = new developmental pathway resulting in fusion of distal radials only posteriorly and articulating distals anteriorly; 3 = return to all distal radials freely articulating with both serially and secondarily associated proximal-middle elements, but retaining a modified articulation with the latter.

Trachinops than in remaining plesiopids. This character might best be considered evidence for Node B.

Homoplasies.—None. Some pseudochromids have a mid-ventral ridge, but this structure maintains a medial position over its entire length and does not divide to meet the lateral edges of the parasphenoid (Fig. 10a). This is a nonhomologous condition.

7. *Slight to Pronounced Notch or Rounded Projection on the Posterolateral Margin of the Exposed Branchiostegal Membranes*

Plesiomorphy.—Outgroups have a smooth posterolateral margin of the branchiostegal membranes. All the more posterior branchiostegal rays curve smoothly dorsally, and are all of approximately the same width (Fig. 11a).

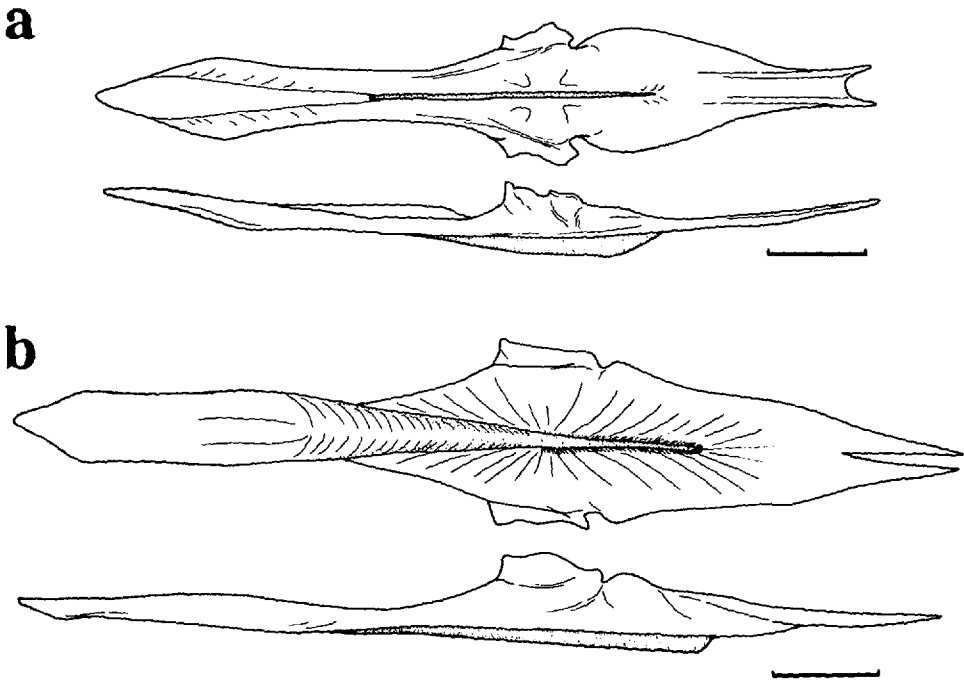


Figure 10. Parasphenoid bones in two pseudochromoids. Keel is stippled. a) Pseudochromine new genus *A. porphyreus* [ROM 1333CS, 38.0 mm], note that keel remains a separate entity; b) *Plesiops coeuruleolineatus* [ROM 776CS, 46.0 mm], note that keel merges anteriorly with lateral ridges of bone. For each, top figure is ventral view and bottom figure is lateral view. Anterior to left. Scale bars are 1 mm.

Apomorphy.—All plesiopids have a slight to pronounced notch or rounded projection on the posterolateral margin of the branchiostegal membranes. This feature was first reported by Smith-Vaniz and Johnson (1990), who noted that the third branchiostegal extends farther posteriorly than the adjacent rays. Gosline (1960) recorded that the third branchiostegal ray of *Plesiops* is “larger” than the other rays, but was not clear as to whether this meant longer or wider. I have found that the length of this third branchiostegal is not appreciably different between outgroups and the ingroup, but that its shape is modified. It is considerably wider than surrounding rays in most plesiopid taxa, especially in *Steeneichthys*. It also becomes straighter distally and does not curve smoothly along with the more posterior branchiostegals (Fig. 11b). This results in the blunt point or notch reported by Smith-Vaniz and Johnson (1990). Although these authors also suggested that *Calloplesiops* lacks the notched membranes, the morphology of the branchiostegals when examined in osteological preparations exhibits the typical plesiopid condition.

Homoplasies.—None. A similar but less pronounced condition exists in *Gramma*. The notch is small, and the ray is not wider than surrounding rays so this is not considered a homologous condition. The branchiostegal notch is also found in gobioids (A. C. Gill, pers. comm.).

8. Preopercular Sensory Canal Open

Plesiomorphy.—The preopercular sensory canal is a closed tube with small foramina leading to the external pores in all outgroups examined (Fig. 12a).

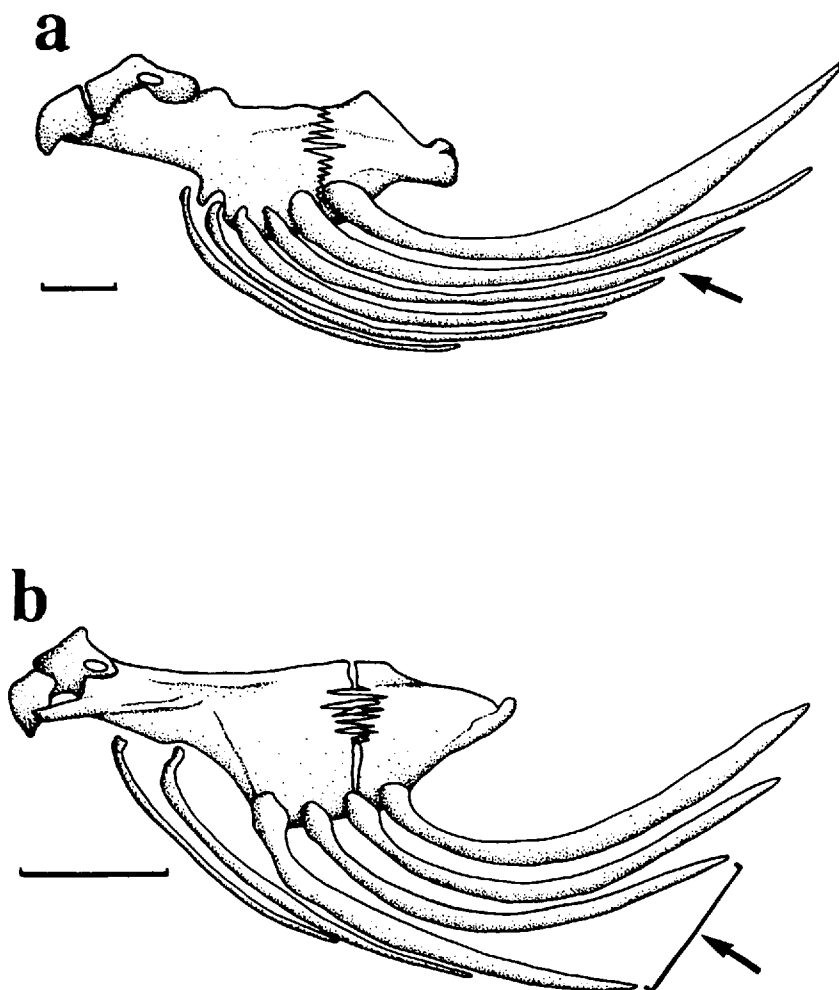


Figure 11. Lateral view of branchiostegal rays of: a) *Labricinus lineatus* [ROM 684CS, 95.0 mm], arrow indicates the close association of third and fourth branchiostegal rays; b) *Assessor macneilli* [USNM 269466CS, 47.5 mm], arrow shows wide gap between third and fourth branchiostegal rays, note also that third ray becomes straight distally. Anterior to left. Scale bars are 2 mm.

Apomorphy.—Plesiopids have open preopercular sensory canals that form what Gosline (1960) first described as a “double border” (Fig. 12b).

Homoplasies.—None. Smith-Vaniz and Johnson (1990) reported the reversal to a closed preopercular sensory canal as evidence that the otherwise derived acanthoclinine genera *Belioops* and *Acanthoplesiops* are sister groups. Members of the family Apogonidae exhibit a very similar condition to that found in plesiopids. This co-occurrence of open preopercular sensory canals is considered convergent, although the possibility of a sister group relationship remains to be investigated.

AUTAPOMORPHIES for *Trachinops*

Monophyly of this genus is supported by a unique caudal-fin shape; the medial rays are produced as a long filament (i.e., a lanceolate condition). *Trachinops* also has an elongate neural spine on preural centrum 2 (pU2), and high numbers of

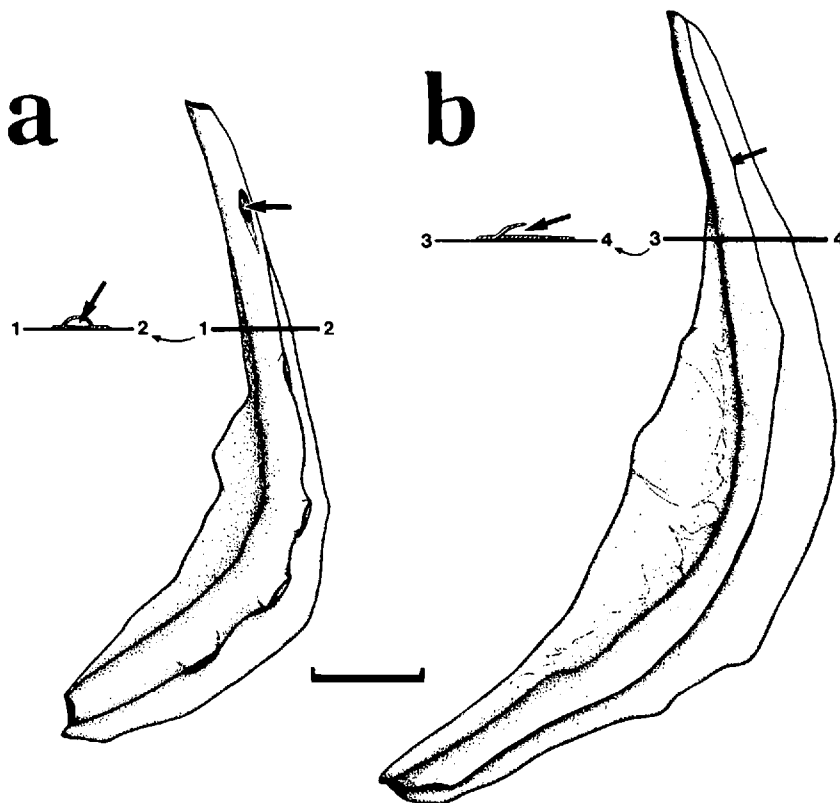


Figure 12. Lateral view of preopercular bones of: a) *Pseudochromis* new genus *A. porphyreus* [ROM 1333CS, 38.0 mm], cross-section 1–2 shows closed sensory canal indicated by arrow, arrow in lateral view points to sensory pore; b) *Plesiops gracilis* [CAS 67423CS, 41.8 mm], cross-section 3–4 shows open sensory canal indicated by both arrows. Anterior to left. Scale bar is 1 mm.

procurent caudal rays in advance of the neural and haemal spines of preural centrum 3 (pU3), conditions not found in other taxa surveyed here (Fig. 13). The elongate body form is rare among plesiopids (found also in some Acanthoclininae), but its polarity is equivocal.

NODE B: Characters 9, 10.1, 11

9. *Small Basioccipital/Parasphenoid Foramen for Dorsal Aorta*

Plesiomorphy.—In most taxa below Node B, the posterior tip of the parasphenoid is U-shaped and a large foramen between it and the basioccipital is present for the passage of the dorsal aorta (Fig. 14a). *Gramma* is somewhat modified from this condition; the parasphenoid is truncated and squared off, not forming the U-shape, but the foramen is still very large.

Apomorphy.—Plesiopid taxa above Node B are characterized by a very small foramen between the basioccipital and parasphenoid (Fig. 14b).

Homoplasies.—Opistognathids also have a small foramen but the structure of the posteroventral portion of the cranium is modified in ways different from that of

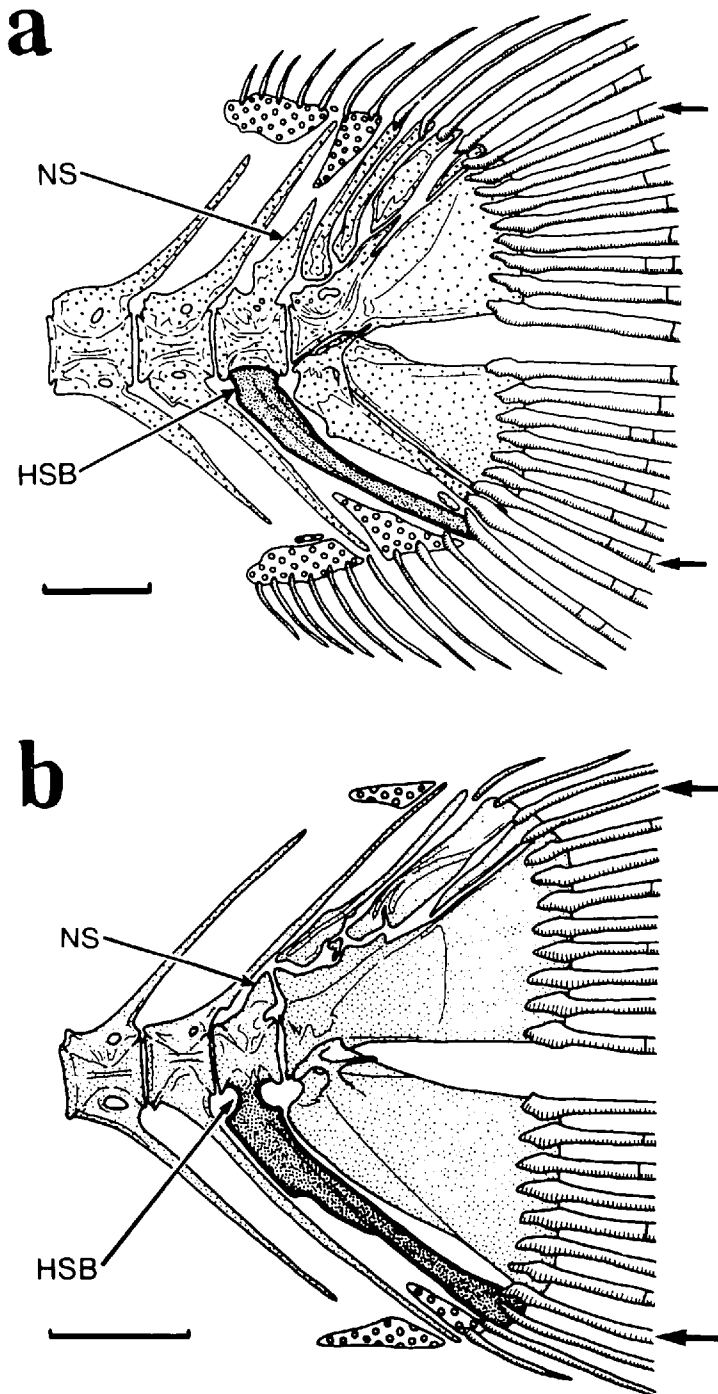


Figure 13. Caudal-fin morphology of: a) *Trachinops noarlungae* [ROM 1332CS, 48.0 mm]; b) *Steenichthys plesiopsus* [ROM 1331CS, 25.8 mm]. Haemal spine of pU2 darkly stippled. NS = neural spine on pU2, HSB = haemal spine base of pU2, short arrows on right point to outermost branched caudal-fin rays. Small open circles represent cartilage. Scale bars are 1 mm.

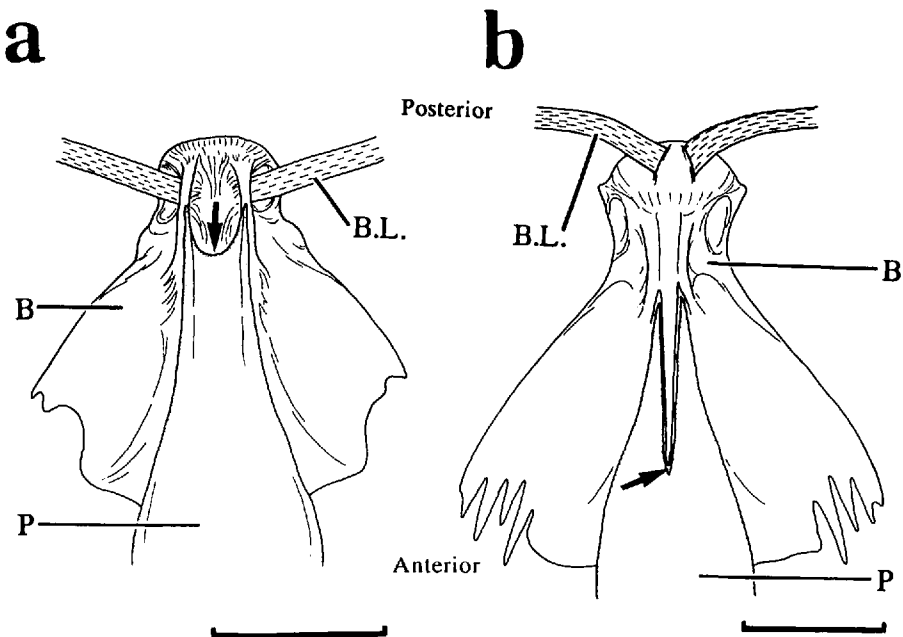


Figure 14. Ventral view of the posterior cranium of: a) *Pseudochromine* new genus *A porphyreus* [ROM 1333CS, 38.0 mm], arrow points into large carotid foramen; b) *Plesiops coeruleolineatus* [ROM 776CS, 46.0 mm], arrow points to small carotid foramen. Posterior towards top. B = basioccipital, B.L. = Baudelot's ligament, P = posterior portion of parasphenoid. Scale bars are 1 mm.

plesiopids or the other outgroups. These differences suggest that the similarly small foramen is a convergent and nonhomologous feature.

10.1. Adductor Superficialis Pelvicus Inserting onto the Spine and only the First Two (or Only First) Segmented Pelvic-fin Rays

Plesiomorphy.—The primitive condition of the adductor superficialis pelvicus is to insert onto the spine and first three or more segmented rays of the pelvic fin. The muscle inserts on all five segmented rays in *Morone*, the first four segmented rays in *Gramma* and the basal pseudochromine new genus *A*, and the first three segmented rays in *Pseudochromis*, *Callanthias*, *Opistognathus*, *Epinephelus*, *Cephalopholis* (Fig. 15a), ambassids, and the plesiopid genus *Trachinops*.

Apomorphy.—In plesiopids above Node B, the adductor superficialis inserts onto the spine and only first and second or only first segmented pelvic-fin ray (Fig. 15b, c).

Homoplasies.—None.

11. Two or Fewer Branches on First Segmented Pelvic-fin Ray

Plesiomorphy.—Outgroups have three or more dichotomous branches of the first segmented pelvic-fin ray. Pseudochromids have 5 or 6 primitively, *Gramma* 3 or 4, *Callanthias* 3, *Morone* 4, and serranids have 4 or more. Most *Trachinops* species have 3 branches of the first ray.

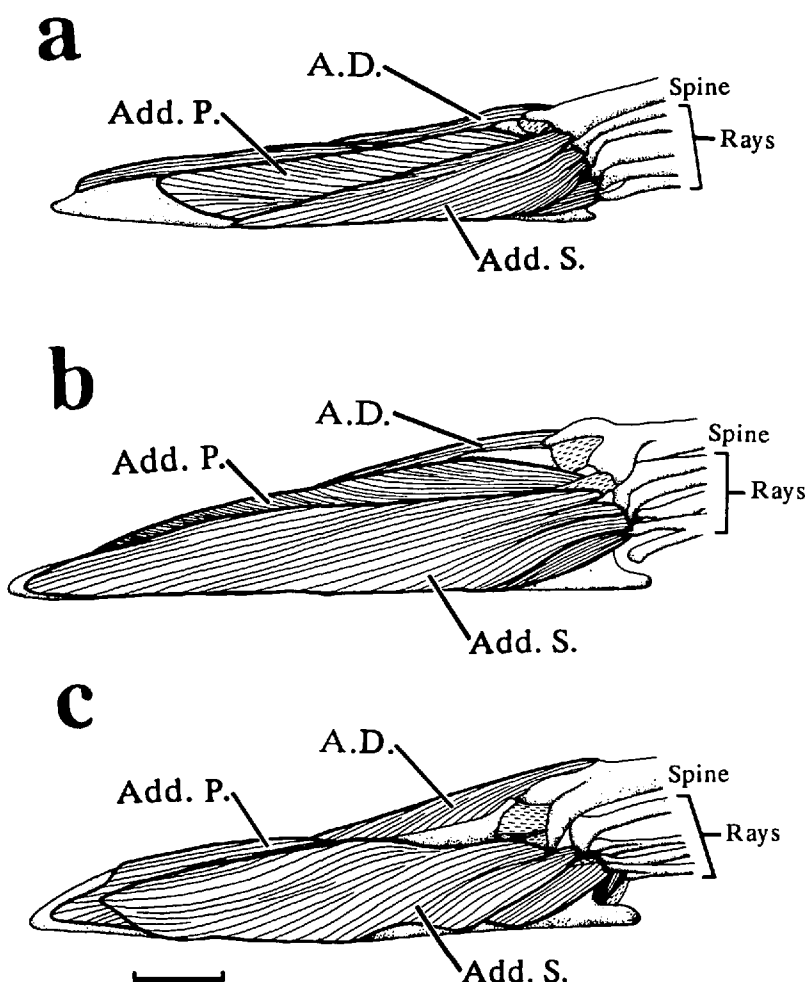


Figure 15. Dorsal view of right pelvic girdle musculature of percoids, extensor proprius removed: a) *Cephalopholis leopardus* [ROM 44656, 80.0 mm]; b) *Paraplesiops poweri* [USNM 274579, 95.0 mm]; c) *Plesiops corallicola* [ANSP 122597, 90.0 mm]. Bold lines demarcate muscles. Broken lines represent tendons. Stippled areas bone. A.D. = arrector dorsalis, Add. S. = adductor superficialis, Add. P. = adductor profundus. Scale bar is 2 mm.

Apomorphy.—Plesiopids above Node B have only 1 or 2 branches on the first segmented pelvic-fin ray.

Homoplasies.—*Opistognathus* has an unbranched first segmented ray. Other more distantly related groups such as some blennioids and gobioids also have reduced numbers of branches on the segmented pelvic-fin rays. However, among lower percoids, this condition appears derived.

AUTAPOMORPHIES for *Assessor*

Assessor has a fully scaled head, including the maxilla. This is a unique feature of this genus among plesiopids and outgroups. Other possible autapomorphies

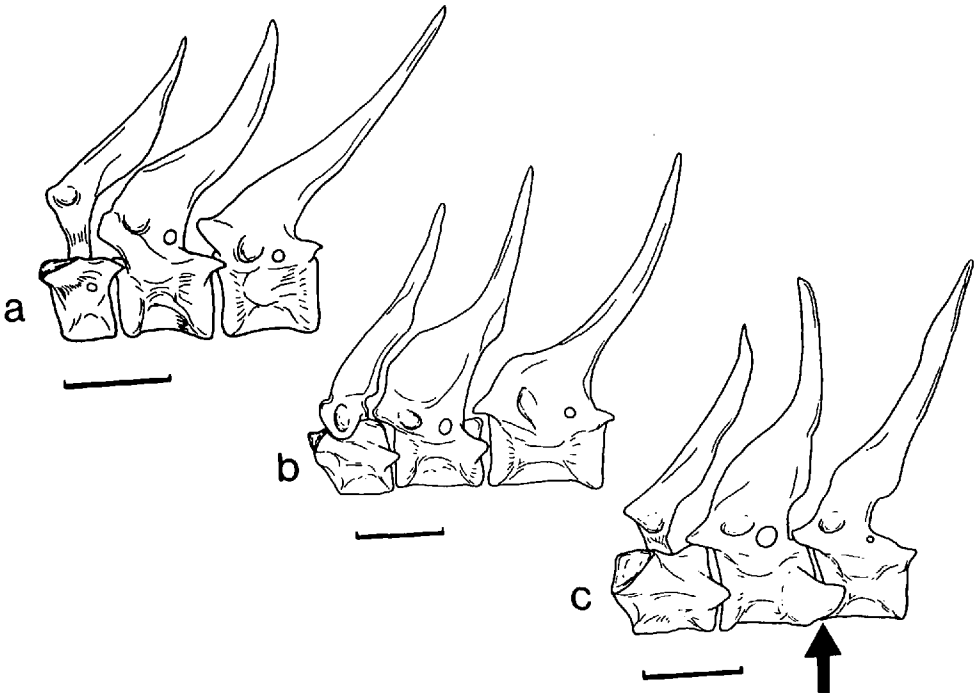


Figure 16. Lateral view of anterior three vertebrae of: a) *Pseudochromine* new genus *A porphyreus* [ROM 1333CS, 38.0 mm]; b) *Assessor macneilli* [USNM 269466CS, 47.5 mm]; c) *Plesiops coeruleolineatus* [ROM 776CS, 46.0 mm]. Anterior to left. Arrow indicates enlarged and ventral zygapophysis. Scale bars are 1 mm.

include the forked caudal fin, toothless vomer, and the curved first anal-fin pterygiophore.

NODE C: Characters 12–15

12. Expanded and Ventrally Positioned Zygapophysis on Second Vertebra

Plesiomorphy.—In most species, the zygapophysis is small and dorsally placed. This is true of *Assessor*, *Trachinops*, and further outgroups (Fig. 16a, b).

Apomorphy.—In genera above Node C, the zygapophysis of the second vertebra is displaced ventrally and has become greatly expanded (Fig. 16c).

Homoplasies.—*Opistognathus darwiniensis* exhibits a somewhat similar morphology, but the structure is not as expanded and not as ventrally positioned. Other opistognathids, such as *O. maxillosus*, do not have this morphology. *Gramma* also has a large zygapophysis on the second vertebra, but again it is not as wide and is not as ventrally placed. I interpret both of these instances as non-homologous similarities.

Smith-Vaniz and Johnson (1990: fig. 18b) illustrated the anterior three vertebrae of *Acanthoplesiops indicus* (Acanthoclininae) and pointed out that the zygapophysis on the second vertebra is reduced (interpreted as a parapophysis in their figure). However, this appears to be a secondarily derived feature, as the reduced

process retains a ventral position and covers the ventral half of the vertebra. This is unlike the condition found in outgroups.

13. *Parasphenoid Deeply Bifurcate Posteriorly*

Plesiomorphy.—In those groups below Node C the posterior tip of the parasphenoid is U-shaped, and there is a large gap between the medial portion of the tip and the basioccipital (Fig. 14a). *Gramma* is slightly modified in that the points of the “U” are absent, and the parasphenoid is truncated.

Apomorphy.—Taxa above Node C all have a deeply bifurcate posterior parasphenoid (Fig. 14b). In addition, there is a triangular ridge of the basioccipital that extends anteriorly between the prongs of the parasphenoid and closes the gap evident in outgroups (Fig. 14).

Homoplasies.—None. In opistognathids, the posterior parasphenoid has a close association with the basioccipital, but, as mentioned in Character 9, the structural arrangement of the posterior cranium appears nonhomologous to that of the taxa above Node B.

14. *Base of Fourth Segmented Pelvic-fin Ray Narrowly Forked, and without an Angular Dorsal Half*

Plesiomorphy.—In outgroups and basal plesiopids, the fourth and/or last (medial) segmented pelvic-fin ray is square shaped, with sharp angles forming the articulation with the pelvic girdle and providing sites for muscle insertion (Fig. 17a–c).

Apomorphy.—Taxa above Node C no longer have a square shaped portion near the proximal tip of the fourth segmented pelvic-fin ray. It remains branched, but forms a simple V-shape with expanded tips for muscle attachment without an angular dorsal half (Fig. 17e–h). This character is not applicable to acanthoclinines, as they have no fourth segmented pelvic-fin ray, as far as I can determine the homology of these elements (see Character 3).

Homoplasies.—*Calloplesiops* appears to exhibit a reversal to the primitive and typical angular dorsal proximal tip to the fourth pelvic ray (Fig. 17d).

Remarks.—It is possible that the shape changes in the tips of the medial pelvic rays might be associated with fusion, or lack thereof, with the middle radial (Character 3; Johnson, 1992). However, the limited ontogenetic series of plesiopids available provide no conclusive evidence of the medial ray fusing with a middle radial.

15. *Membranes of Dorsal-fin Spines Incised*

Plesiomorphy.—Outgroups and plesiopids below Node C have the spinous portion of the dorsal fin with membranes running the full length of the spine, except occasionally the extreme distal tip.

Apomorphy.—Most taxa above Node C have incised membranes in the spinous portion of the dorsal fin. The membranes often extend only half, or sometimes less, of the length of the spine.

Homoplasies.—*Calloplesiops* and *Fraudella* have apparently reversed this con-

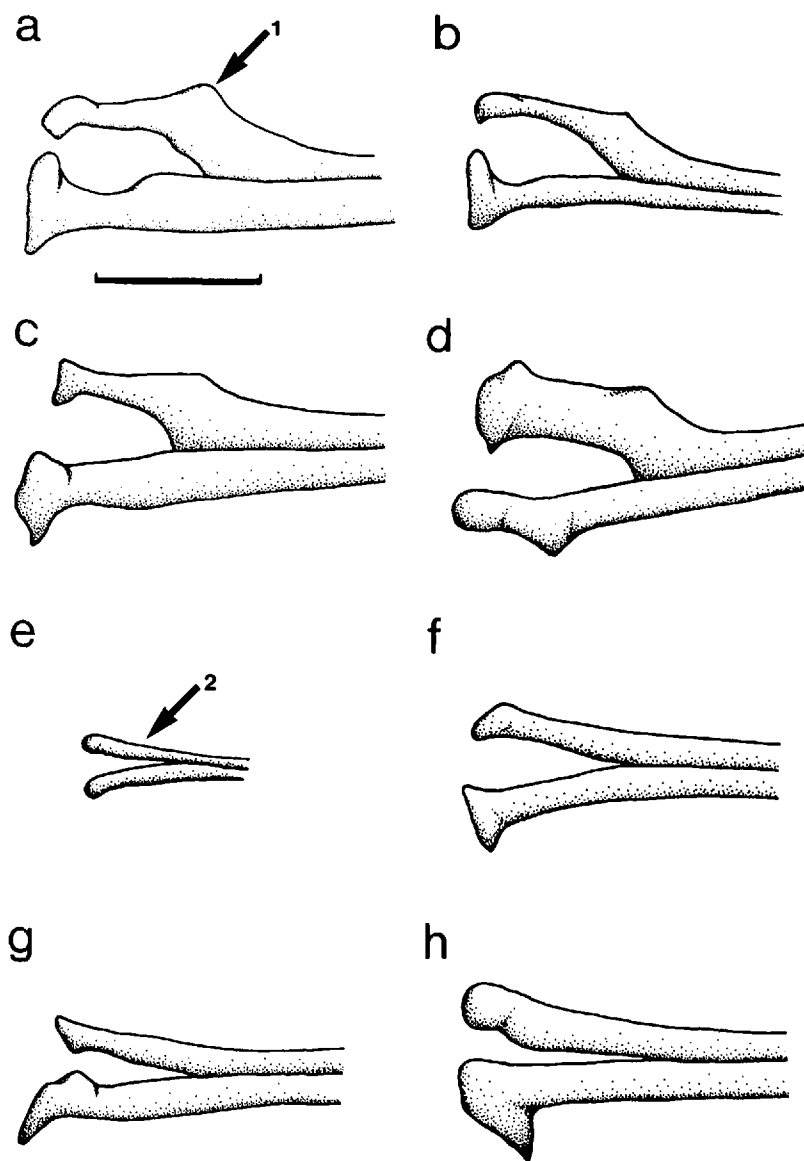


Figure 17. Proximal tips of medial pelvic rays of: a) *Pseudanthias* sp. [ROM 775CS, 52.0 mm], fifth ray; b) Pseudochromine new genus *A. porphyreus* [ROM 1333CS, 38.0 mm], fourth ray; c) *Assessor macneilli* [USNM 269466CS, 47.5 mm], fourth ray; d) *Callopleksiops altivelis* [ROM 894CS, 50.0 mm], fourth ray; e) *Steeneichthys plesiopsus* [ROM 1331CS, 25.8 mm SL], fourth ray; f) *Paraplesiops poweri* [USNM 274578CS, 47.8 mm], fourth ray; g) *Fraudella carassiops* [QM 1.19760CS, 45.0 mm], fourth ray; h) *Plesiops coeruleolineatus* [ROM 776CS, 46.0 mm], fourth ray. Medial view, anterior to left. Arrow 1 indicates the angular dorsal portion present in a–d; arrow 2 notes the absence of the angular portion as in e–h. Scale bar is 1 mm in a, and 0.5 mm in b–h.

dition to the primitive state. In the former, a functional (though weak) “explanation” might exist for the reversal, as McCosker (1977) has suggested that this species is a Batesian mimic of a moray eel. An incised dorsal fin might reduce the similarity of the mimic with its model.

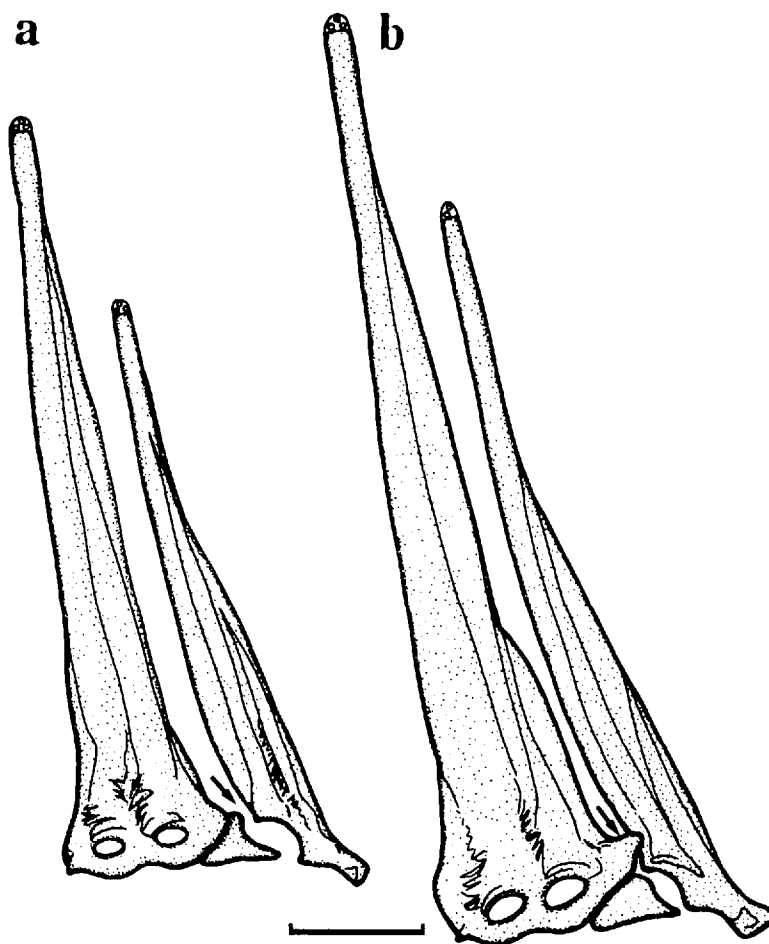


Figure 18. Anterior two anal-fin pterygiophores of: a) *Plesiops gracilis* [CAS 67423 CS, 41.8 mm], arrow indicates absence of an articulation of the pterygiophores; b) *Paraplesiops poweri* [USNM 274578CS, 47.8 mm], arrow points to the articulation between the two pterygiophores. Anterior to left. Small open circles represent cartilage. Scale bar is 1 mm.

NODE D: Character 16

16. Proximal-middle Radial of First Anal-fin Pterygiophore is in Contact with the Second Anal-fin Pterygiophore

Plesiomorphy.—In all plesiopids other than those above Node D, and in some outgroups such as *Gramma* and opistognathids, the first and second anal-fin pterygiophores are not in contact with one another (Fig. 18a).

Apomorphy.—In the genera *Steeneichthys*, *Calloplesiops*, and *Paraplesiops*, the first anal-fin pterygiophore is in contact with the second (Fig. 18b). This is particularly obvious in the latter genus, where a distal process of the first pterygiophore bears a groove in which a portion of the second pterygiophore rests.

Homoplasies.—This character is difficult to polarize with confidence, as both states occur in the outgroups. Primitive pseudochromids and *Morone* exhibit the apo-

morphic condition as here defined. FIG/FOG analysis suggests that this polarization is correct, as the sequential outgroup genera to other plesiopids, *Trachinops* and *Assessor*, both have separated first and second anal-fin pterygiophores. However, the equivocal nature of this character suggests that Node D is only a tentative hypothesis.

AUTAPOMORPHIES for *Paraplesiops*

Monophyly of this genus remains to be conclusively demonstrated, although the interpretation of the dorsal spine-bearing pterygiophore development outlined under Character 5 (Remarks) provides one autapomorphy. The five included species are very similar meristically and are easily distinguished from other genera, but the meristic data are a unique combination of primitive counts, perhaps excepting number of vertebrae (26–27 vs. 25 in most other plesiopids and outgroups). *Paraplesiops* is most similar to *Callopleysiops* osteologically, sharing numerous features, but these are apparently symplesiomorphies. It remains a possibility that this genus is paraphyletic or even polyphyletic.

NODE E: Characters 17–19

17. Lower Lip Complete, not Interrupted by Isthmus

Plesiomorphy.—Pseudochromids, opistognathids, and plesiopids except those at Node E and acanthoclinines have incomplete lips. The isthmus interrupts the lip at the symphysis of the lower jaw.

Apomorphy.—In *Steeneichthys* and *Callopleysiops* the lower lip is complete and not interrupted at symphysis.

Homoplasies.—This is a variable character among many of the taxa examined in this study. Pseudochromids have an incomplete lower lip primitively, although the character exhibits at least one reversal within this group, and is polymorphic in some species (Gill, 1990). The acanthoclinines have been defined in part by the presence of a complete lower lip (Smith-Vaniz and Johnson, 1990). Because of this variability, I hesitate to use this character as evidence for relationships.

18. Low Total Caudal-fin Ray Count

Plesiomorphy.—Outgroups and most plesiopids have 26 or more caudal-fin rays: *Gramma* has 29, basal pseudochromids have 28 or more, *Trachinops* and *Assessor* over 30, *Paraplesiops* 29, and *Plesiops* 26 or more (Fig. 13a).

Apomorphy.—Both *Callopleysiops* and *Steeneichthys* have reduced the number of caudal-fin rays to 23 (Fig. 13b).

Homoplasies.—Among outgroups, *Opistognathus* has reduced the number of caudal rays to 23. Within the ingroup, acanthoclinines have also reduced the number of rays to 24 or fewer.

19. Basal Constriction in the Haemal Spine of pU2

Plesiomorphy.—Outgroups and plesiopids other than *Callopleysiops* and *Steeneichthys* have a broad articulation of the haemal spine with the pU2 centrum that gradually narrows distally to form the spine (Fig. 13a).

Apomorphy. — *Callopleles* and *Steeneichthys* both have a pU2 haemal spine that is constricted proximally before returning to a more usual width distally (Fig. 13b).

Homoplasies. — None.

AUTAPOMORPHIES for *Callopleles* and *Steeneichthys*

Callopleles is a monotypic genus, hence monophyletic. Its color pattern, a black body with white spots and an ocellus on the dorsal fin, is unique. It does not appear to belong among any of the other plesiopid taxa, although it shares many plesiomorphic osteological features with *Paraplesiops*. As the potential sister group to *Steeneichthys*, its generic status can be maintained without interfering with classifications reflecting phylogeny while providing taxonomic stability.

Steeneichthys species are diminutive, and might be progenetic. Unique, possibly paedomorphic features include the single tubed lateral-line scale and simple (unbranched) first segmented pelvic-fin ray. Tubed lateral-line scales are replaced posteriorly by scales with sensory papillae, unique to this genus within the Plesiopidae. *Steeneichthys* also has a bulb of tissue at the symphysis of the lower jaw found among other plesiopids only in derived acanthoclinines (e.g., *Belonepterygion*). They also share with most acanthoclinines the unusual condition of a fused hemal spine on the second preural centrum. Unique internal morphology includes the basiptyergium which is a high arched structure. The cranium has an ossified interorbital septum formed by thin plate-like extensions of the frontals, parasphenoid, basisphenoid, and pterosphenoids. Contrary to observations of Allen and Randall (1985: 187), the palatine bears teeth, so "absence of palatine teeth" is not an autapomorphy.

NODE F: Characters 20–22

20. Three Anteriormost Vertebrae with Relatively Smooth Ventral Surfaces

Plesiomorphy. — All taxa below Node F have thin, ventrally directed ridges or shelves as far anteriorly as the second vertebra (Fig. 19a, b).

Apomorphy. — In the taxa above Node F, the ventral ridges are absent on the first three vertebrae, which are relatively smooth and unsculptured ventrally (Fig. 19c).

Homoplasies. — None. Derived acanthoclinines of the genus *Acanthoplesiops* have an apparently reversed condition, where the anterior vertebrae regain ventrally directed ridges (Smith-Vaniz and Johnson, 1990: fig. 18b).

21. Posteroventral Attachment of Baudelot's Ligament to the Basioccipital

Plesiomorphy. — In outgroup taxa, and those plesiopids below Node F, Baudelot's ligament attaches to the basioccipital in a lateral fossa, the actual attachment point not being visible from a ventral view (Fig. 14a).

Apomorphy. — *Fraudella*, *Plesiops*, and acanthoclinines have a more ventral attachment of Baudelot's ligament to the basioccipital, onto a medial, triangular, slightly raised process (Fig. 14b).

Homoplasies. — Opistognathids have a similar condition to that found in Node F taxa. Differences in parasphenoid and basioccipital shape between these taxa make me reluctant to accept homology between these structures. The Node F taxa are

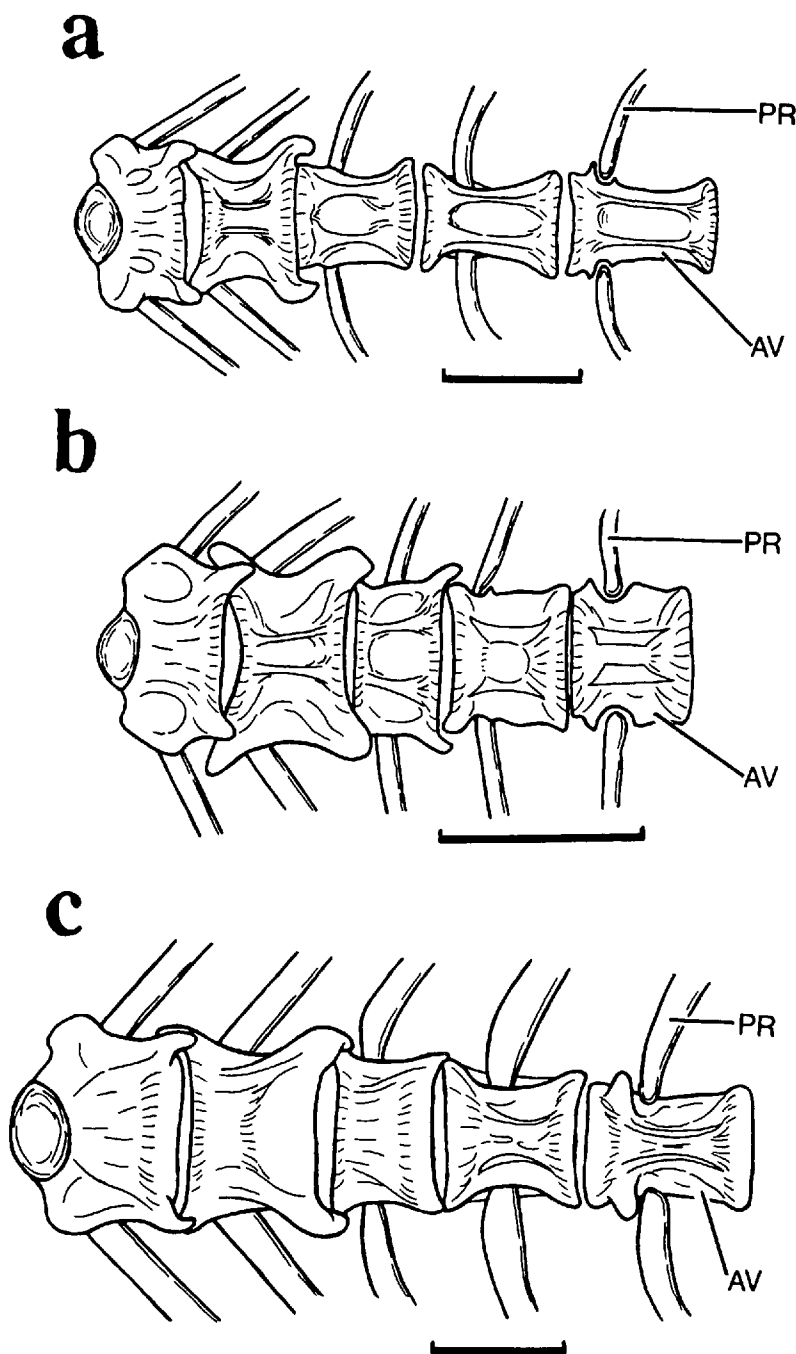


Figure 19. Ventral view of anterior five vertebrae of: a) *Pseudochromine* new genus *A. porphyreus* [ROM 1333CS, 38.0 mm], only first vertebra with a relatively smooth ventral surface; b) *Steeneichthys plesiopsus* [ROM 1331CS, 25.8 mm], only first vertebra with a smooth ventral surface; c) *Plesiops gracilis* [CAS 67423CS, 41.8 mm], first three vertebrae with smooth surfaces. Anterior to left. AV = centrum of abdominal vertebra, PR = pleural rib. Scale bars are 1 mm.

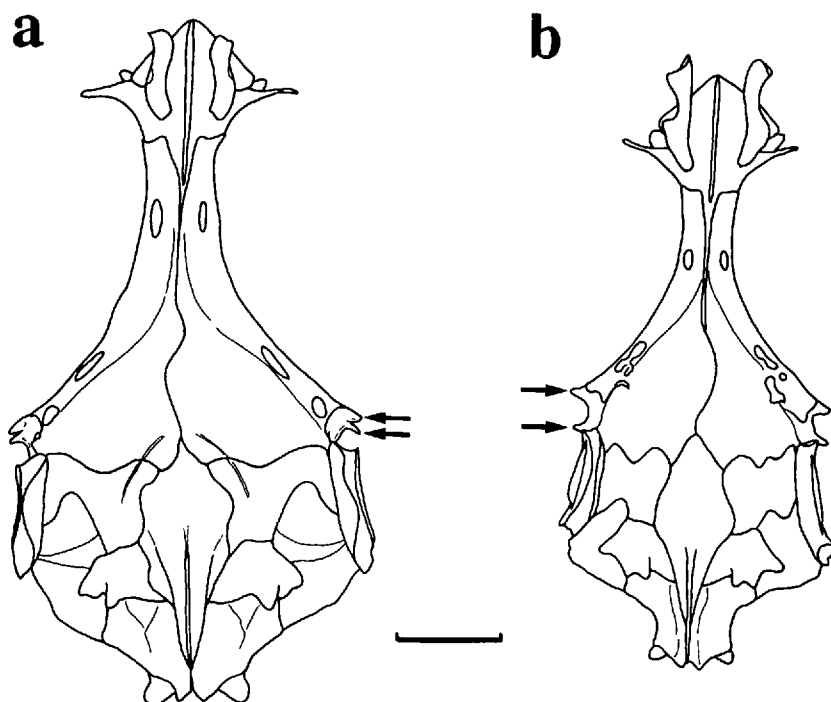


Figure 20. Dorsal view of the crania of: a) *Paraplesiops poweri* [USNM 274578CS, 47.8 mm], arrows indicate proximity of the sphenotic processes; b) *Plesiops gracilis* [CAS 67423CS, 41.8 mm], arrows indicate distance between sphenotic processes. Anterior at top. Scale bar is 1 mm.

quite deep within the plesiopid cladogram, and one could argue that opistognathids and these groups are too distantly related to permit an hypothesis of homology for this character. I treat this feature as consistent (i.e., not homoplastic) among plesiopids.

22. Posterior Sphenotic Spur Widely Separated from the Anterior Spur

Plesiomorphy.—The posterior sphenotic spur is very small and very closely associated with the anterior sphenotic spur in outgroups and plesiopids below Node F (Fig. 20a).

Apomorphy.—In *Fraudella*, *Plesiops*, and acanthoclinines, the posterior sphenotic spur is large and widely separated from the anterior spur (Fig. 20b). This condition is most extreme in the acanthoclinines.

Homoplasies.—None. The genus *Rypticus*, an epinepheline serranid in the tribe Grammistini, also has a posterior sphenotic spur that is widely separated from the anterior spur, but this group is unrelated to those discussed here, and homology between these similar states is highly unlikely.

AUTAPOMORPHIES for *Fraudella*

Fraudella is monotypic and unique among plesiopids in having preopercles serrated for much of their length and very broad infraorbital bones.

NODE G: Characters 10.2, 23–25

10.2. *Adductor Superficialis Pelvicus Inserts onto the Spine and First Segmented Pelvic-fin Ray Only*

Plesiomorphy.—The primitive condition of this transformation series has the adductor superficialis inserting onto the spine and first three or more segmented rays (Fig. 15a). The second state, Character 10.1, has the muscle inserting only onto the spine and first two rays (Fig. 15b).

Apomorphy.—The derived state at this node of the cladogram is an insertion of the adductor superficialis onto the spine and first segmented ray only (Fig. 15c).

Homoplasies.—*Steeneichthys* also has a reduced insertion of the adductor superficialis to only the spine and first segmented ray of the pelvic fin.

23. *Abductor Superficialis Pelvicus Does Not Overlie the Arrector Ventralis Pelvicus Posterior to the Infracarinalis Anterior*

Plesiomorphy.—In outgroup taxa, the abductor superficialis pelvicus extends laterally (to the iliac spur in plesiopids below Node G) to overlie the arrector ventralis muscle posterior to the overlying infracarinalis anterior. In *Epinephelus*, *Cephalopholis*, *Morone*, *Gramma*, and primitive pseudochromids, the arrector ventralis is almost completely obscured by the abductor superficialis (Fig. 21a), but in “lower” plesiopids the abductor superficialis extends as a thin sheet laterally and covers only the more anterior portions of the arrector ventralis (Fig. 21b).

Apomorphy.—In *Plesiops* and acanthoclinines, the muscle fibers of the abductor superficialis run longitudinally and do not extend laterally to the iliac process. Hence, it does not overlie the arrector ventralis posterior to the infracarinalis anterior (Fig. 21c).

Homoplasies.—Only opistognathids have a similar condition to taxa above Node G. Other characters, including those of the pelvic girdle (such as absence of a subpelvic shelf), suggest that the structure in opistognathids has had a separate history from plesiopid taxa. FIG/FOG analysis suggests that the similarity in abductor superficialis morphology is a convergent feature, and not homologous.

24. *Dorsal Process for Muscle Attachment Large Only on First Segmented Pelvic-fin Ray*

Plesiomorphy.—On plesiopids below Node G (excluding *Steeneichthys*) and in outgroups, the dorsal surfaces of at least the first two segmented pelvic-fin rays have large proximal expansions for muscle attachment (Fig. 22a). The more medial rays often only have small knobs or processes for this purpose.

Apomorphy.—Taxa above Node G have a large proximal expansion for muscle attachment only on the first segmented pelvic-fin ray (Fig. 22b). More medial rays may have smaller processes.

Homoplasies.—The number of large proximal expansions on the dorsal surface of the pelvic rays appears to be correlated with the number of rays onto which the adductor superficialis inserts. *Steeneichthys*, along with *Plesiops* and acanthoclinines, has only one expanded flange and has the adductor superficialis inserting only onto that ray. This suggests that the flange character is homoplastic and that it is linked to Character 10.1 of Node B. The first is true and the character is

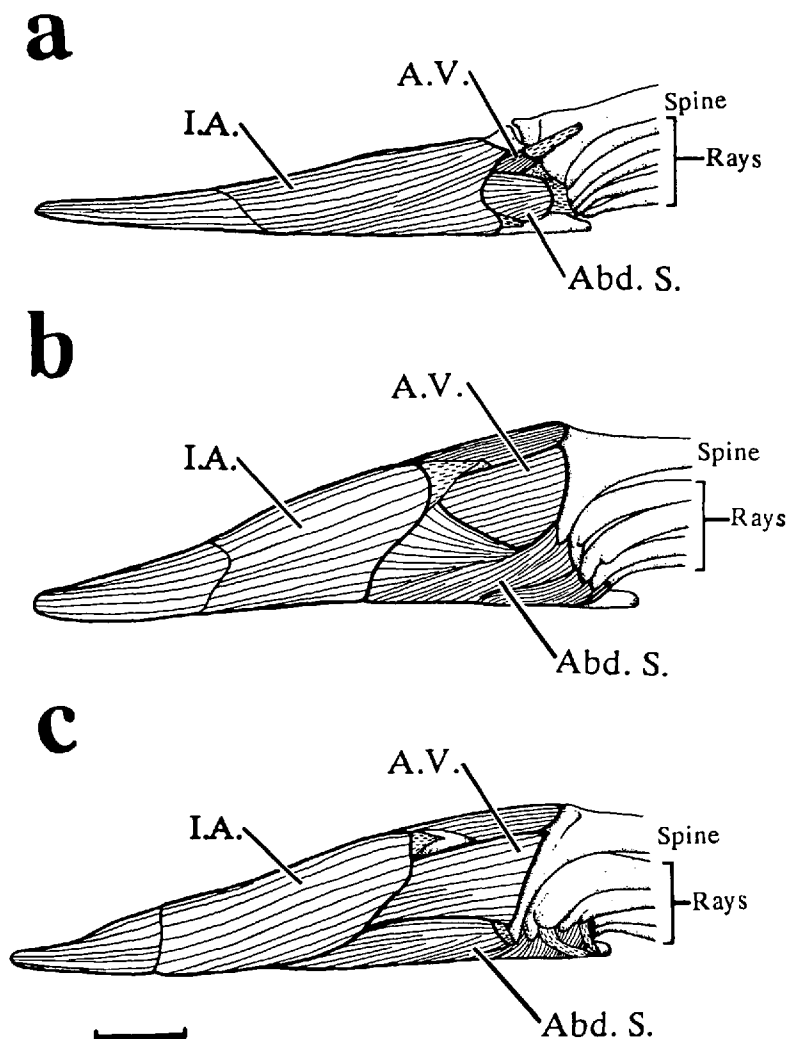


Figure 21. Ventral view of the left pelvic girdle musculature of: a) *Cephalopholis leopardus* [ROM 44656, 80.0 mm]; b) *Paraplesiops poweri* [USNM 274579, 95.0 mm]; c) *Plesiops corallicola* [ANSP 122597, 90.0 mm]. Bold lines demarcate muscles. Broken lines represent tendons. Stippled areas are bone. Anterior to left. Abd. S. = abductor superficialis, A. V. = arrector ventralis, I.A. = infracarinalis anterior. Scale bar is 2 mm.

homoplastic, but *Assessor* has large flanges on the outer segmented pelvic-fin rays and the adductor superficialis muscle inserts only onto the first two of these, indicating that the two characters can change independently of one another.

25. *No Lateral Processes on the Posterior (Middle Radial) Portion of the Proximal-middle Radial of the Dorsal Spine-bearing Pterygiophores*

Plesiomorphy. — The most posterior tip of the dorsal spine-bearing pterygiophores has lateral wing-like processes that, in outgroups, forms a cradle for the articulating distal radial (Fig. 3a). In most plesiospids, these lateral processes are still developed despite the loss of articulation with the distal radial (Figs. 23a, 24a).

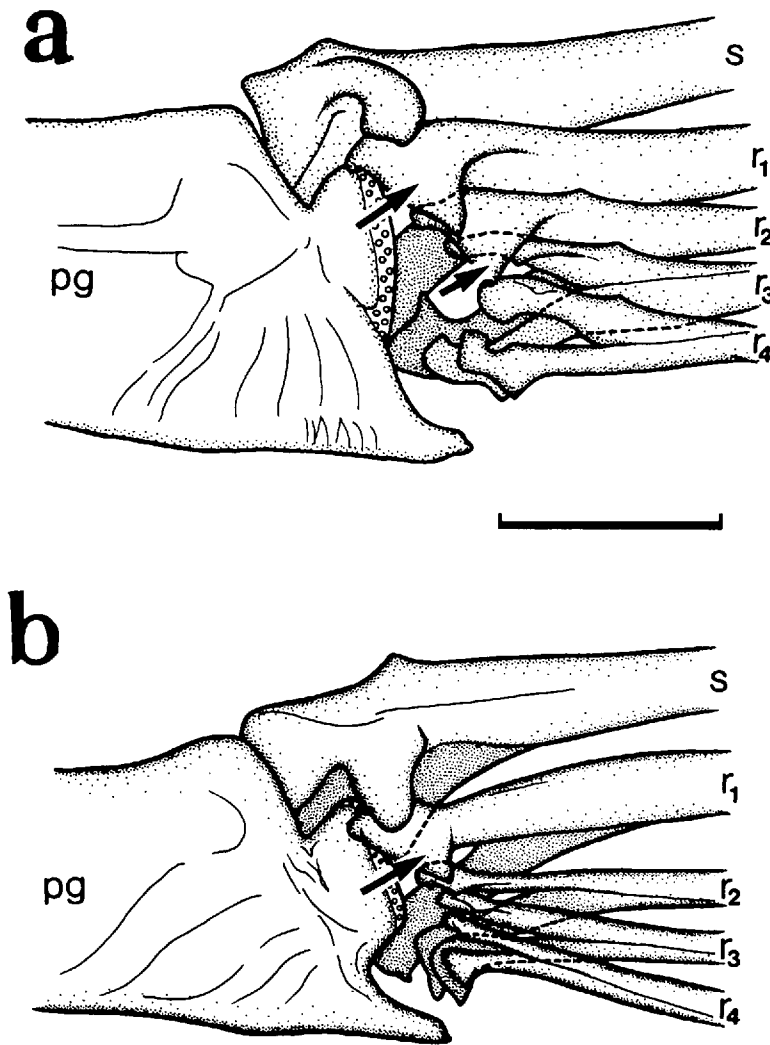


Figure 22. Dorsal views of the proximal tips of the pelvic fin rays of: a) *Callopleysiops altivelis* [ROM 894CS, 50.0 mm]; b) *Plesiops coeruleolineatus* [ROM 776CS, 46.0 mm]. Anterior to left. Arrows point to large dorsal processes for muscle attachment, two in a, one in b. Open circles represent cartilage. pg = pelvic girdle, s = spine, r1-r4 = rays one to four. Scale bar is 1 mm.

Apomorphy. — *Plesiops* and acanthoclinines have lost the lateral processes on the posterior portion of the proximal-medial radials of the dorsal spine-bearing pterygiophores. They have a thin, pointed, posteriorly-directed process with no lateral projections (Figs. 23c, 24b).

Homoplasies. — *Trachinops* has a condition similar to that found in *Plesiops* and acanthoclinines (Fig. 23b).

AUTAPOMORPHIES for *Plesiops* and Acanthoclininae

This monophyly of *Plesiops* is presently being investigated with a revision of the genus. The acanthoclinines have been demonstrated to be monophyletic based

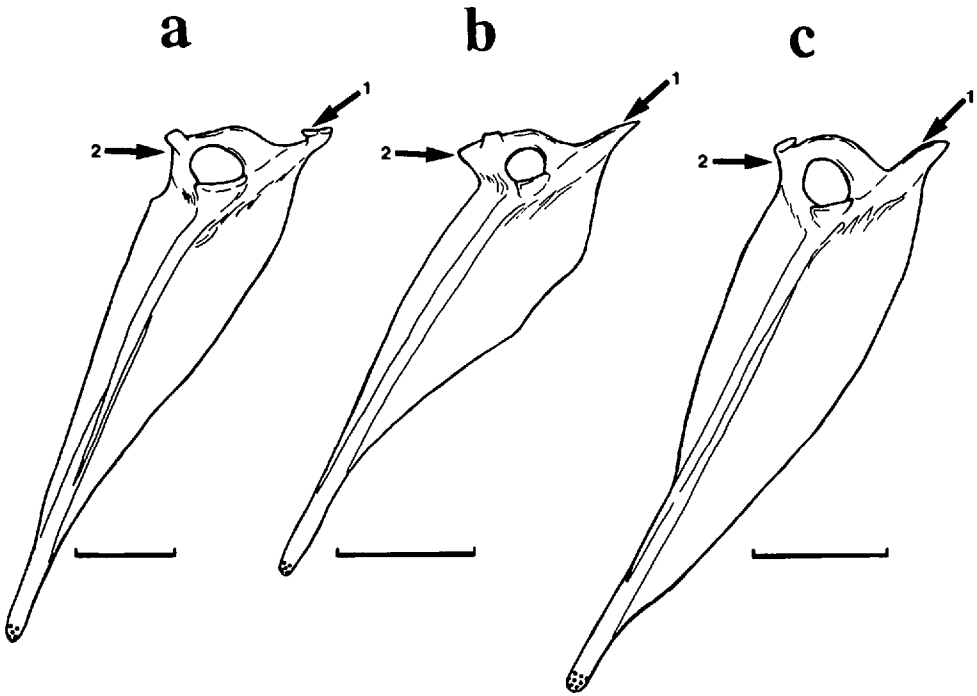


Figure 23. Lateral views of fifth dorsal-fin spine-bearing pterygiophores of: a) *Steeneichthys plesiopsus* [ROM 1331CS, 25.8 mm], arrow 1 points to the posterior lateral process, arrow 2 indicates the absence of the anterior process; b) *Trachinops noarlungae* [ROM 1332CS, 48.0 mm], arrow 1 indicates the absence of the posterior lateral process, arrow 2 points to the anterior process; c) *Plesiops coeruleolineatus* [ROM 776CS, 46.0 mm], arrow 1 notes the absence of the posterior lateral process, arrow 2 indicates the absence of the anterior process. Anterior to left. Stippling represents cartilage. Scale bars are 0.5 mm in a–b, and 1 mm in c.

on five features as outlined by Smith-Vaniz and Johnson (1990): 1) lower lip continuous, 2) head naked, 3) dorsal and anal fins with increased numbers of spines and concomitant decrease in number of rays, 4) reduced number of pelvic-fin rays (to 2), and 5) reduction in number of branched caudal-fin rays to 14 in adults. The first of these is homoplastic (see Character 17), and the fifth is shared with some individuals of *Steeneichthys*. I have found another potential autapomorphy for the subfamily, discussed under Character 4, namely the absence of an extensor proprius pelvis muscle.

26. Loss of the Anterior Process of the Distal Radial

Plesiomorphy.—All taxa but *Plesiops* and *Steeneichthys* retain the anterior process of the distal radial that primitively articulated with its serially associated proximal-medial radial, despite the loss of this articulation (Fig. 23b).

Apomorphy.—Both *Steeneichthys* and *Plesiops* have lost the anterior process of the distal radial (Figs. 23a, c, 24).

Homoplasies.—The occurrence of this apomorphic condition in these two taxa is apparently independent if the phylogeny presented in Figure 1 is correct. *Steeneichthys* is a highly derived, probably progenetic genus that might not develop the

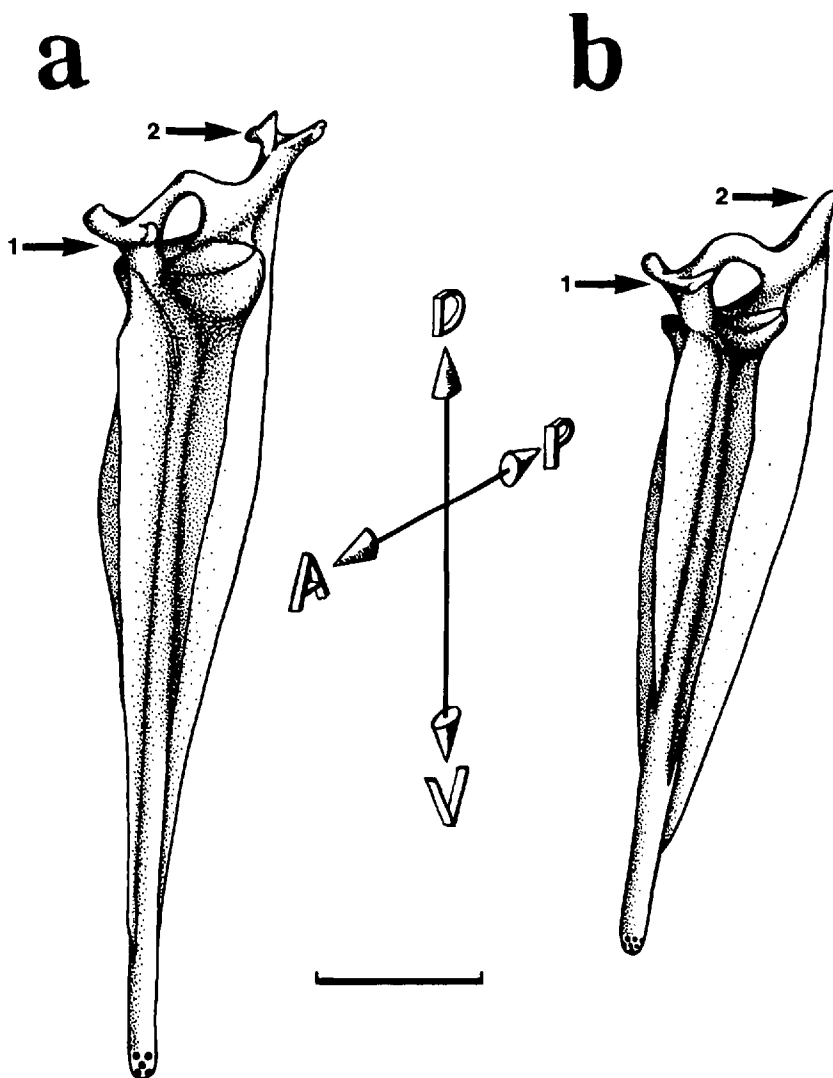


Figure 24. Three dimensional view of fifth spine-bearing dorsal pterygiophores of: a) *Steeneichthys plesiopsus* [ROM 1331CS, 25.8 mm], arrow 1 indicates absence of anterior process, arrow 2 notes right posterior lateral process; b) *Plesiops coeruleolineatus* [ROM 776CS, 46.0 mm], arrow 1 indicates absence of anterior process, arrow 2 indicates absence of posterior lateral processes. Larger dark spots represent cartilage. Orientation compass—A = anterior, P = posterior, D = dorsal, V = ventral. Scale bar is 0.5 mm in a, and 1 mm in b.

anterior process because of its pedomorphic development. If this is correct, it would be evidence that the similar states in these taxa are nonhomologous.

A summary of character codings as described above is presented in Table 1.

DISCUSSION OF PHYLOGENY

The monophyly of the Plesiopidae + Acanthoclinidae is well-supported by at least seven characters (Character 6 might be considered evidence of Node B) (Fig. 1). However, relationships among the taxa of this clade remain somewhat am-

Table 1. Data matrix for phylogenetic analysis of the Plesiopidae. Characters 1–8 are autapomorphies for the family not used for calculation of tree statistics. Symbols: 0 = plesiomorphic state; 1 = apomorphic state; ? = uncertain polarity; – = character not applicable; 0–1 = both states present in different outgroups

Taxon	Character																			
	1–5					6–10					11–15					16–20				
Outgroup	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0–1	0	0	0	0
<i>Trachinops</i>	1	1	1	1	1	1?	1	1	0	0	0	0	0	0	0	0	0	0	0	1
<i>Assessor</i>	1	1	1	1	1	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Paraplesiops</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0
<i>Callopleysiops</i>	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	1	0	0
<i>Steeneichthys</i>	1	1	1	1	1	1	1	1	2	1	1	1	1	1	1	1	1	1	0	1
<i>Fraudella</i>	1	1	1	1	1	1	1	1	1	1	1	1	1	0	0	0	0	1	1	0
<i>Plesiops</i>	1	1	1	1	1	1	1	1	2	1	1	1	1	1	0	0	0	0	1	1
<i>Acanthoclininae</i>	1	1	1	1	1	1	1	1	2	1	1	1	–	1	0	0	1	0	1	1

biguous despite the fact that PAUP found only one tree with the branch-and-bound option. The consistency index of the tree, not including basal synapomorphies, is 0.68 (28 steps with a minimum of 19). This is above that which could be expected for a matrix of randomly generated data of this size (Klassen et al., 1991). The retention index is 0.84. However, I would argue that some of the consistent characters (particularly 12 and 13 of Node C, and 20 and 21 of Node F) provide reasonable hypotheses of the general picture of relationships. With such characters, and the seven basal autapomorphies, the acanthoclinids (sensu Hardy, 1985) are placed deeply within the clade, and it would take a good deal of contrary (and consistent) evidence to remove them from this position.

If the cladogram is taken at face value, it provides a solution to a problem regarding the evolution of reproductive modes in plesiopids. There has been some discussion whether mouth-brooding is primitive or derived within pseudo-chromoid fishes. Thresher (1984) suggested that the occurrence of spherical egg masses in non-mouthbrooding fishes is evidence that oral incubation is the primitive condition for the group, and Mooi (1990) contested that such a statement remains speculation until a phylogeny of these fishes is hypothesized. The cladogram in Figure 1 is such an hypothesis for part of this group. Within plesiopids, *Trachinops* and *Acanthoclinus* produce spherical egg masses, and this is likely to be the case for *Paraplesiops* and *Fraudella* (which have similar eggs to those of *Trachinops*). *Assessor* is the sole taxon known to be a mouthbrooder. If the phylogeny hypothesized in Figure 1 is correct, it indicates that oral incubation is an autapomorphy for *Assessor* and that the primitive condition for the group is the production of a spherical egg mass. This contention is testable, as further evidence can contradict or support the current phylogeny and, in turn, refute or support the polarity of reproductive behavior in these fishes. The homology of egg surface morphologies in plesiopids remains an enigma, despite the occurrence of very similar and complex structures in some groups. Surprisingly, the similar egg morphologies of *Paraplesiops*, *Trachinops*, and *Fraudella* described by Mooi (1990) do not seem to be indicative of a close relationship among these genera. The condition found in *Plesiops* of numerous filaments encircling the micropyle (Mito, 1955; Mooi, 1990) is an apparent autapomorphy for the genus within the Plesiopidae.

The relationships of taxa in Figure 1 also suggest that schooling is primitive

for plesiopids (both *Trachinops* and *Assessor* are schooling forms), and that small size (ca. 50 mm SL) is plesiomorphic. Relatively large size (> 150 mm SL) appears to have arisen independently on three occasions: once in a single species of *Plesiops*, in *Paraplesiops*, and in one genus of acanthoclinine, *Acanthoclinus*.

The problem of affinities of the Plesiopidae with other families of the Percoidei could not be resolved by the present study. No evidence was found to support the hypothesis of Mok et al. (1990) that the Plesiopidae are the sister group to a monophyletic Pseudochromidae + (Opistognathidae + Grammatidae). The exact relationship of the Plesiopidae to other perciforms awaits further investigation.

A Revised Classification of the Plesiopidae. — If it is desirable to have a taxonomic system that reflects current knowledge of relationships, then the phylogeny presented has implications for the taxonomy of these fishes. Clearly, the Plesiopidae as conceived in the recent literature are paraphyletic. As noted above, despite some doubt about relationships among the included taxa, the Acanthoclinidae (sensu Hardy, 1985) are well-established as a member of a plesiopid + acanthoclinid assemblage. Following Smith-Vaniz and Johnson (1990), who based their decision on the work presented above and on my recommendation, I have synonymized these taxa under the name Plesiopidae to recognize the revised monophyletic family.

The information concerning interrelationships of the included taxa should also be retained in a classification. The most widely accepted procedure for accurately portraying the branching pattern of a phylogeny in a classification is the sequencing convention (Nelson, 1974; Wiley, 1979, 1981). To apply this method, the taxa to be sequenced must be of equivalent rank. To comply with this rule, I have raised the rank of the genera *Trachinops*, *Assessor*, *Fraudella*, *Plesiops*, and the group *Calloplelesiops* + *Steeneichthys* + *Paraplesiops* to the subfamilial level, and lowered the rank of the former Acanthoclinidae (sensu Hardy, 1985) to this same subfamilial stature. This arrangement, one of many possible, maintains the previous taxonomy to some degree by retaining a high rank for the acanthoclinid genera (sensu Hardy, 1985). The sequencing convention has also been applied to genera within the subfamilies; the phylogeny of the acanthoclinine genera follows Smith-Vaniz and Johnson (1990). The newly constructed classification follows:

Family PLESIOPIDAE Günther, 1861

Subfamily TRACHINOPINAE, new

Trachinops Günther, 1861

Subfamily ASSESSORINAE, new

Assessor Whitley, 1935

Subfamily PARAPLESIOPINAE, new

Paraplesiops Bleeker, 1875

Calloplelesiops Fowler and Bean, 1930

Steeneichthys Allen and Randall, 1985

Subfamily FRAUDELLINAE, new

Fraudella Whitley, 1935

Subfamily PLESIOPINAE Günther, 1861

Plesiops Cuvier, 1816

Subfamily ACANTHOCLININAE Günther, 1861

Acanthoclinus Jenyns, 1842

Belonepterygion McCulloch, 1915

Beliops Hardy, 1985

Acanthoplelesiops Regan, 1912

Portions of the cladogram upon which the classification is based are tentative. The monophyly of the Paraplesiopinae is supported by a single character (Character 16: Fig. 1), and resolution of relationships among the Fraudellinae, Plesiopinae, and Acanthoclininae involves some homoplastic features (Fig. 1). Consequently, it is possible that internal organization of both the cladogram and classification will require modification with the analysis of additional characters.

Diagnosis of the Revised Plesiopidae.—A diverse group of fishes having: incomplete or disjunct lateral lines; pelvic fin combination of I,4 or I,2; a notch in the posterolateral margin of the branchiostegal membranes just dorsal to the third branchiostegal ray, this ray usually being the widest and most robust of six; branchiostegal membranes usually visible beyond the subopercle and opercle; basipterygium with a well-developed subpelvic shelf originating from the main lateral strut; a subpelvic concavity present posterior to bases of the subpelvic processes; extensor proprius pelvici inserting onto second segmented pelvic-fin ray (except in Acanthoclininae where this muscle is absent); dorsal spine-bearing pterygiophores interlocking with spines via a closed ring of bone formed by fusion of the distal radials with the proximal-middle radials of the secondarily associated pterygiophores (except in some members of *Paraplesiops* which have free distal radials, a condition similar to the plesiomorphic percoid state, but likely non-homologous); preopercular sensory canal open (except for some derived acanthoclinines); parasphenoid keel present; hypurals 1 and 2 (and sometimes parhypural) fused into autogenous plate, hypurals 3 and 4 fused to each other and to urostylar complex.

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